

Devonian vertebrates from the Canning and Carnarvon Basins with an overview of Paleozoic vertebrates of Western Australia

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A diverse vertebrate fauna, comprising both micro- and macrovertebrate remains, is known from the Paleozoic of Western Australia. However, it is the Late Devonian fauna of the Gogo Formation that shows exceptional preservation and which is the best known. Advances in tomographic techniques, both micro-CT and synchrotron, have revealed new histological data providing information on bone growth, muscle attachments and the evolution of teeth. The fishes from the Gogo Formation have also revealed new information on the evolution of reproductive structures and live birth in early vertebrates. Recent work on the Frasnian reefs that crop out along the Lennard Shelf and mineral drillcore through Paleozoic sedimentary rocks have yielded scales of agnathan thelodonts, and the bones, teeth and scales of sharks, acanthodians and osteichthyans, all of which have increased our knowledge of Ordovician–Late Devonian microfaunas in the Canning Basin, contributing to our understanding of biostratigraphy and correlation within Australia and globally. Less work has been undertaken in the Carnarvon Basin, although like the Canning Basin this has concentrated on Late Devonian strata. More recently, work has commenced on describing Early Carboniferous faunas from the Canning, Carnarvon and Bonaparte Basins. All this work is providing information on faunal patterns and exchange of vertebrates through the Paleozoic. However, the paleogeographic evidence provided by the vertebrates is sometimes at odds with paleogeographic reconstructions based on paleomagnetic evidence and further investigation is required to resolve these differing interpretations.

KEYWORDS: biostratigraphy, early vertebrates, East Gondwana, Lagerstätten, paleogeography, Paleozoic.

INTRODUCTION

Paleozoic fossil fishes of Western Australia, particularly those from the Gogo Formation Lagerstätten located in the Canning Basin, have been invaluable for investigating major evolutionary transitions due to the exceptional preservation and diversity of the fauna. The gnathostomes (jawed vertebrates) recovered from the Gogo Formation in the Kimberley region comprise members of all the major groups and demonstrate key evolutionary shifts from the development of jaws and teeth, the first expression of live-young bearing in vertebrates, to the emergence of stem tetrapods. However, and unlike many other sites in the State, to date no jawless vertebrates have been recovered from this site. In contrast to the excellent preservation found in the fossils of the Gogo Formation, those from the more southerly Carnarvon Basin are disarticulated but show high faunal diversity.

In Western Australia the fossil record of Paleozoic fishes includes both microvertebrate and macrovertebrate remains (Long & Trinajstic 2000, 2010; Burrow *et al.* 2010). The majority of the research conducted to date has been on Devonian, especially Late Devonian marine faunas, with studies on Ordovician, Silurian,

Carboniferous and Permian fossils less common. There are no reports of Cambrian vertebrate fossils from Western Australia, although rare, purported vertebrate fossils of this age are known from deposits in central Australia (Young *et al.* 1996). Studies on Western Australian Ordovician to Early Devonian taxa are restricted to microvertebrate faunas recovered from mineral drillcore. However, the extensive outcrops of Devonian reefs in the Canning Basin are rich in both macro- and microvertebrate faunas and numerous studies on both have been undertaken.

In the early 20th century predominantly morphological descriptions and taxonomic studies were undertaken. In the latter part of the 20th century research began to focus on biostratigraphy, particularly in the areas of marine–non-marine correlation under the UNESCO:IUGS IGCP328 Paleozoic Microvertebrates project led by Alain Blicek, Susan Turner and Gavin Young (Blicek & Turner 2000). Unlike many of the currently used invertebrate zone fossils including conodont elements, Paleozoic fish often occur in transitional environments, with the same species inhabiting marine, nearshore and/or non-marine facies. Some marine units bearing microvertebrates are extremely well dated through tying the vertebrate faunas to standard conodont zonations (Trinajstic & George 2009). In continental rocks microvertebrates are often the only age indicators preserved. Since 1980 there has been

a systematic effort to recover microvertebrate remains from Gondwanan Paleozoic rocks from Australia and neighbouring countries (Long 1990; Turner 1982a, b, 1991, 1993, 1997; Vergoossen 1995; Young 1986, 1987; Basden *et al.* 2000; Young & Turner 2000; Burrow 2002; Macadie 2002; Burrow *et al.* 2010; Young *et al.* 2010).

Morphological studies of macrovertebrates have recently taken the forefront again with the advent of new computerised tomographic techniques, allowing for the first time non-destructive histological ‘sectioning’ of dermal plates and *in situ* teeth and scales at high resolution. The fossils from the Gogo Formation have been significant in the utilisation of these new technologies in answering questions on the evolution and development of teeth (Rücklin *et al.* 2012) and scales (Qu *et al.* 2013a, b), muscle attachments to bone (Sanchez *et al.* 2012, 2013), soft tissue preservation (Trinajstic *et al.* 2013) and reproduction in vertebrate animals (Long *et al.* 2008, 2009; Ahlberg *et al.* 2009; Trinajstic & Johanson 2014; Trinajstic *et al.* in press a).

Knowledge of the diversity and stratigraphy of vertebrate faunas from the three Paleozoic basins in Western Australia is variable, with some faunas, e.g. the Gogo fauna, having been more studied than others, e.g. the Moogooree Limestone and Utting Calcarenite faunas. However, recent research has given greater insights into the diversity, taxonomy, phylogeny and biogeographic relationships of the Western Australian faunas and

indicates differences from the longer-studied faunas in central and eastern Australia.

CANNING BASIN

The Paleozoic Canning Basin is characterised by deposition of fine-grained marine clastics and carbonates on extensive carbonate platforms and marine shelves (Cadman *et al.* 1993). Vertebrate fossils are known from Ordovician to Carboniferous sedimentary rocks. One of the most studied areas is the Upper Devonian reef complexes, which are well exposed along the Lennard Shelf and form a belt ~350km long and up to 50km wide (Hocking *et al.* 2008). However, the units can be discontinuous at times, narrow and devoid of complete sections due to margin collapse, as is evident in the Napier Range (Shen *et al.* 2008).

The Frasnian strata of Western Australia, especially those in the Canning Basin, have had more numerous studies undertaken on them than those in other areas and ages, yielding a variety of macro- and microvertebrate fossils (Long 1993). The strata are divided into a number of formations representing different reef facies, some of which are laterally equivalent. For example, the contemporaneous Gogo, Sadler and Pillara formations represent basinal, slope and backreef facies, respectively (Playford *et al.* 2009).

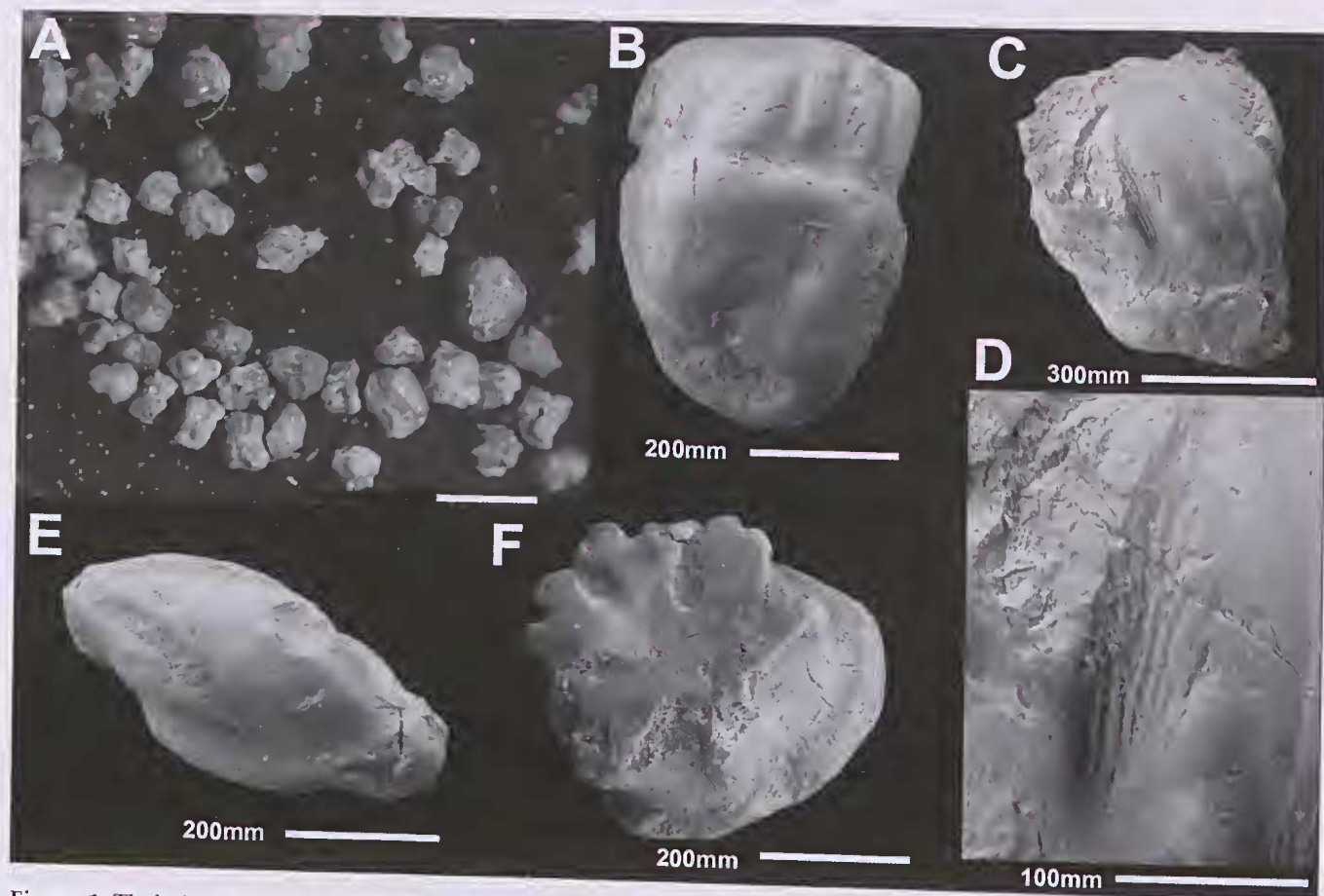


Figure 1 Thelodont scales from Wilson Cliffs 1, Kidston Sub-basin. (A) Isolated scales with grains of quartz attached. (B) Eroded head scale in lateral view. (C) Body scale in anterior view showing linear microornament. (E) Body scale in lateral view. (F) Head scale in crown view. (D) Detail of microornament.

The best known of these in respect to vertebrate fauna is the early Frasnian Gogo Formation, which represents the basinal facies of the reef complex (Long & Trinajstić 2010). This fauna is represented exclusively by macroremains.

The Virgin Hills Formation extends from the lower Frasnian to the uppermost Famennian and represents both basinal and reef slope facies (Playford *et al.* 2009). Rare macrovertebrate remains, mostly of isolated placoderm plates, have been recovered from the Famennian part of the measured section whereas microvertebrates are common from the Frasnian and Famennian reef-slope facies (Trinajstić & Long 2009; Hansma *et al.* in press).

VERTEBRATE FOSSILS OF THE CANNING BASIN

Ordovician

The first description of an Ordovician fish from the Canning Basin was based on fragmentary dermal armour in core recovered from Kidson 1 well, attributed to a new genus and species of arandaspid (jawless fish) *Ritcheichthys nibili* (Sansom *et al.* 2013). Prior to this discovery, reports of Ordovician vertebrate taxa from Australia, including remains from Early to mid-Ordovician, were restricted to marginal marine deposits in central and southeast Australia (Ritchie & Gilbert-Tomlinson 1977; Young 1991, 1997, 2009). Arandaspid

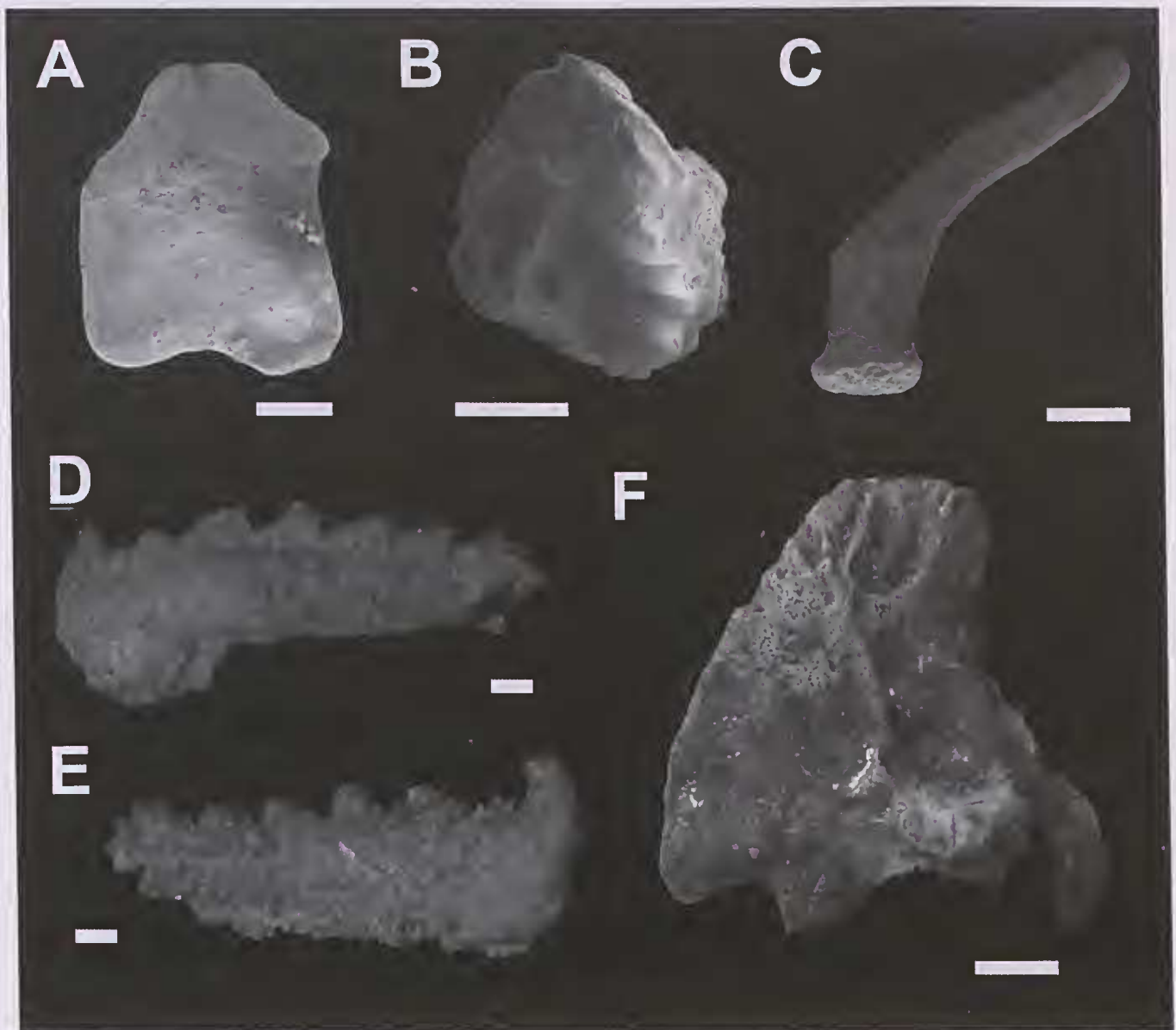


Figure 2 Givetian vertebrate remains from the Cadjebut Formation, Canning Basin. (A) Chondrichthyan tooth gen. et sp. indet., in labial view. (B) Chondrichthyan scale in crown view. (C) Placoderm neural spine. (D, E) Arthrodire infragnathal biting division; (D) left lateral view, (E) right lateral view. (F) Ptyctodont left preorbital plate in visceral view. Scale bar: 0.5 mm in A–C; 0.1 mm in D–E; 5 mm in F.

fishes are also known from central South America (Bolivia) (Gagnier *et al.* 1996) and Oman in the Arabian peninsula (Sansom *et al.* 2009) indicating a perigondwanan distribution in a narrow, nearshore environment. This is part of the Gondwanan Evolutionary Assemblage of Blicek & Turner (2003) and Turner *et al.* (2004).

Silurian

Fossil vertebrates from the Silurian of Western Australia are represented solely by microfossils recovered from boreholes. These primarily comprise thelodont and acanthodian micro-remains with rare scales attributed to actinopterygians. Upper Silurian horizons in Pendock 1A well yielded scales tentatively attributed either to the thelodont *Loganellia* sp. cf. *L. grossi* (V N Karatjute-Talimaa pers comm. 1994) or more probably cf. *Niurolepis* sp. (personal observation ST) and acanthodian *Nostolepis* cf. *alta* and ?stem actinopterygian *Andreolepis*. These taxa suggest correlation with the Late Silurian (Ludlow) in Iran and northern Europe and suggest a relative closeness between northern Gondwana and Laurentia, rather than any massive oceanic barrier at this time.

Upper Silurian horizons in Kempfield 1 yield scales similar in morphology to *Thelodus parvidens* from Avalonia and Laurentia, and in addition those from a possible Silurian level in Gingerah Hill 1 resemble other European loganelliids and *Niurolepis susanae* from Iran, although these have not yet been formally described (Burrow *et al.* 2010; Turner 2014).

There are no known later Ordovician to Early Silurian vertebrates anywhere in Australia probably because of the Hirnantian into Early Silurian glaciation (Turner *et al.* 2004).

Devonian

EMSIAN–EIFELIAN

Early Devonian (late Pragian?–Emsian) scales of the thelodont *Turinia australiensis* (Figure 1A–F) and unnamed acanthodians were described from the Wilson Cliffs 1 borehole (Gross 1971) from the Tandalgoo Red Beds (now named Tandalgoo Formation), a unit underlying the well-known reef complexes of the southern Canning Basin. The recognition of thelodont scales led to the re-dating of the strata from Permian to Early Devonian, demonstrating the utility of microvertebrates in dating rocks in the absence of conodonts, or where conodonts are undiagnostic. The type material was redescribed and refigured by Turner (1995). The assemblage also includes placoderm dermal scales and bone fragments, an onychodont tooth and a

single shallow-marine unidentified conodont element (personal observation, CJB, ST). Turner (1997) reviewed known records of *T. australiensis* in relation to conodont data across Australia.

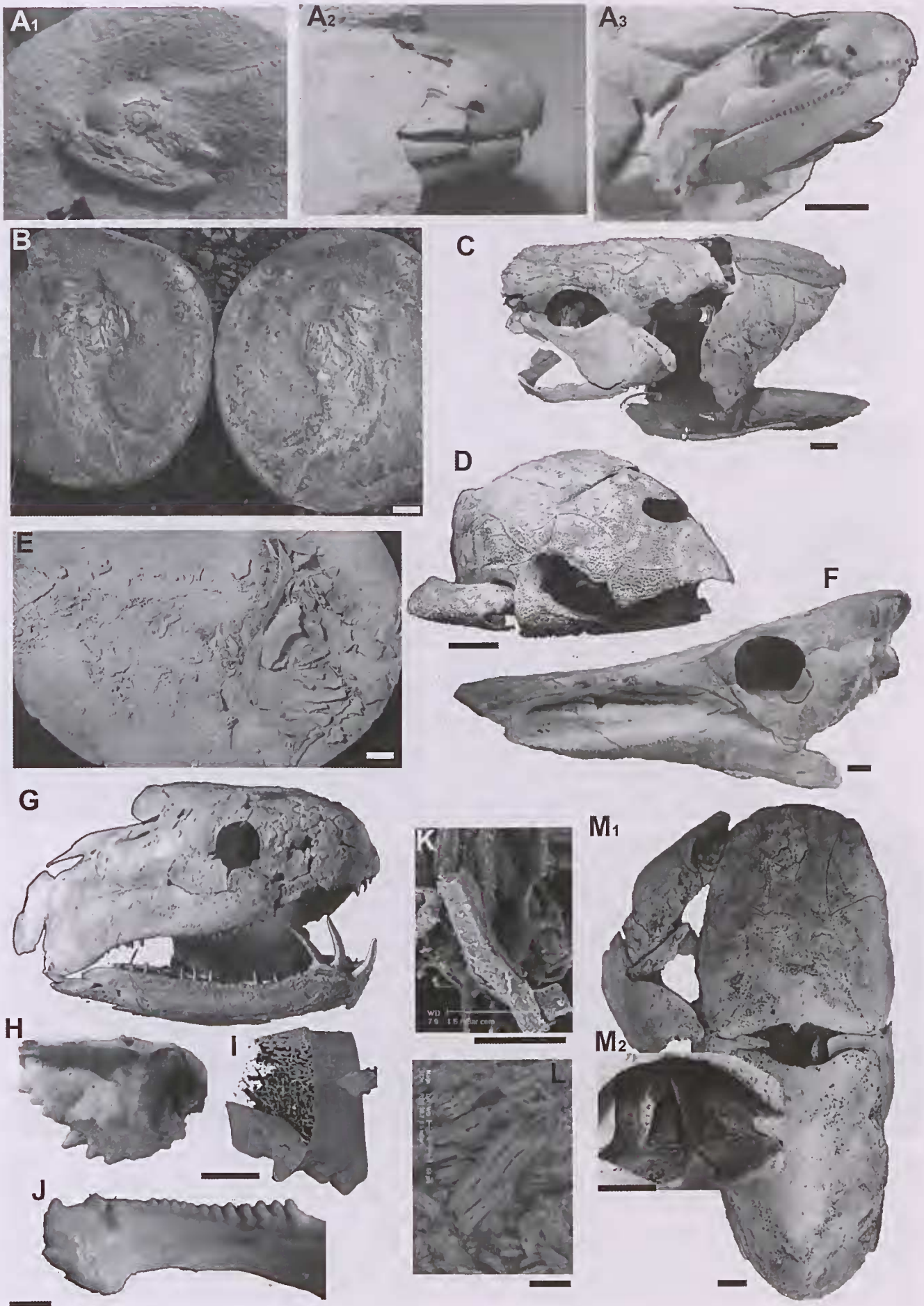
GIVETIAN

The Givetian Cadjebut Formation represents a restricted marine environment and to date only a small number of invertebrate fossils of low diversity have been reported. In 2010 isolated toothplates were recovered by Peter Haines (GSWA) and identified (by KT) as those of a ptyctodont placoderm. Further collecting in 2011 yielded a single chondrichthyan tooth of indeterminate affinity (Figure 2A) and chondrichthyan scales (Figure 2B). Additional 3D-preserved placoderm material was also collected including vertebral elements (Figure 2C), dermal plates and tooth plates (Figure 2D, E) representing new genera and species of arthrodires, and dermal plates from the headshield of a ptyctodont (Figure 2F). Elsewhere in Australia, placoderm remains are common components in Lochkovian to Famennian strata throughout eastern Australia (Young 1993; Parkes 1995; Turner *et al.* 2000; Burrow 2003), as well as in early Givetian strata in the MacDonnell Ranges of central Australia (Young *et al.* 1987; Young & Goujet 2003; Young 2005). Their rarity in Lower Devonian strata of Western Australia is possibly a result both of lack of outcrop as well as lack of exploration.

FRASNIAN

The first fishes were collected from the Gogo Formation in the 1940s by Curt Teichert who identified placoderm fossils, which he recognised as being similar in morphology to the European coccosteids (Long 2006). It was not until Harry Toombs from the British Museum (Natural History) (BMNH) visited the University of Western Australia in 1955 and was given material to prepare using his new acetic acid technique that the full extent of this find was realised (Figure 3A_{1,3}). The limestone concretions were found to contain fossils preserved in 3D with the original bones intact and undistorted (Figure 3B). Toombs returned and represented the BMNH in two major expeditions, which systematically collected fish and crustaceans from the Gogo Formation in 1963 and 1967, in collaboration with the Western Australian Museum and Hunterian Museum (Glasgow, Scotland). The Gogo Formation has to date yielded 45 species of fish (Long & Trinajstić 2010), the majority being arthrodire placoderms (25%) (Figure 3C), with antiarchs (10%) (Figure 3D), and ptyctodonts (5%) (Figure 3E), recovered in lesser numbers. Of the osteichthyans, palaeoniscoids (Figures 3B, 5C, D) represent the next most abundant group (24%), followed

Figure 3 Vertebrate remains from the Gogo Formation, Canning Basin. (A_{1,3}) *Gogonaspis andrewsae* head at various stages of acetic acid preparation. (B) A split nodule in the field containing a palaeoniscoid in part and counterpart. (C) Arthrodire *Incisoscutum ritchei* head and trunk shield in lateral view. (D) Head and trunk shield of *Bothriolepis* sp. (E) *Austroptyctodus gardineri* (counterpart) in lateral view. (F) Head of *Griphognathus whitei* in lateral view. (G) *Onychodus jaudemarrai* in lateral view. (H) *Compagopiscis croucheri* upper toothplate in ventral view. (I) CT scan of upper toothplate of *Compagopiscis croucheri* showing histological detail; (J) lower toothplate of *C. croucheri* in lateral view. (K) Mineralised muscle fibres from the arthrodire *Incisoscutum ritchei*. (L) Mineralised biofilm surrounding muscle fibres in *Eastmanosteus calliaspis*. (M) *Eastmanosteus calliaspis* with nuchal gap musculature preserved; (M₁) detail of nuchal gap musculature. Scale bar: 1 cm in A–J, M; 50 µm in K, L.



by dipnoans (20%) (Figure 3F), and osteolepiforms (2%) (Figure 3G). More recently, a single acanthodian was described by Burrow *et al.* (2012). In addition two sharks and a coelacanth have been prepared but await full description. Long & Trinajstić (2010) gave a recent review of the faunal composition and so only a brief overview of discoveries post-2010 will be presented here.

With the advent of new technologies, including micro CT and synchrotron tomography, the first non-destructive examinations of histological structures of the fishes from the Gogo Formation have been undertaken (Long *et al.* 2008; Sanchez *et al.* 2013; Trinajstić *et al.* 2013). The ontogenetic history is largely conserved within the dermal bones preserved as lines of arrested growth (Sanchez *et al.* 2012, 2013). This characteristic has enabled changes in growth of the jaws to be ascertained and led to significant advances in our understanding of the development of teeth (Figure 3H–J) in some early jawed vertebrates (Smith & Johanson 2003; Rücklin *et al.* 2012). The presence or absence of teeth in placoderms has been a controversial topic, particularly since the proposition by Smith & Johanson (2003) that teeth were secondarily developed in arthrodire placoderms from ‘toothless’ ancestors. Synchrotron scans of the jaws of an arthrodire (*Compagopiscis*) showed the pulp canal within each tooth became infilled during growth (Rücklin *et al.* 2012). This discovery supports Smith & Johanson’s (2003) hypothesis that the dental structures in arthrodires are true teeth, and teeth might have evolved at least twice in early vertebrate evolution. Studies on the antiarch *Bothriolepis* (Figure 3D) show tooth-like structures on biting surfaces that are consistent with the histology of the dermal armour, further indicating that teeth and jaws may not have evolved simultaneously (Rücklin *et al.* 2012), as antiarchs are considered to be basal phylogenetically to arthrodires (Zhu *et al.* 2013).

Reconstructing the soft anatomy of extinct animals has often been a pipe dream in paleontology, and has until recently mostly relied on functional interpretation and the preservation of muscle scars on the skeleton. The interolateral plate (= clavicle) of placoderms was hypothesised to be the site of the coracobranchialis muscle (Johanson 2003). Synchrotron studies of the interolateral plate from *Compagopiscis* a placoderm from Gogo revealed the presence of numerous embedded extrinsic fibres indicating muscle attachment points. The principal fibre alignments are anteroposterior in the anterior part of the attachment and anterodorsal in the more dorsal part indicating the presence of two muscles (Sanchez *et al.* 2012), where previously only one muscle had been predicted (Heintz 1930; Miles 1969; Johanson 2003). Changes in the distribution of osteocyte lacunae within the bone indicated where deep entheses (connective tissue between the tendon and the bone) of tendon-attached muscles formed, often leaving a muscle scar on the external bone, whereas more shallow muscle insertions left no muscle scars (Sanchez *et al.* 2012). These superficial muscle entheses had not previously been predicted on the basis of visual examination of the bone and so the number of muscles present in these extinct organisms has been underestimated (Trinajstić *et al.* 2012). Thus not only can the synchrotron reveal the site of muscle attachment but also the type of attachment. This technique, pioneered on Gogo fish, has made the

reconstruction of soft anatomy far more accurate than previously realised.

The exceptional preservation of fossils in the Gogo Formation is not restricted to the preservation of bone but includes mineralised muscles also preserved in 3D, in placoderms, chondrichthyans and palaeoniscoids. Initially only small amounts of muscle were recovered from under the dermal plates of the headshield (Figure 3K, L), which had collapsed onto themselves forming a closed micro-environment providing the condition conducive to soft-tissue preservation (Trinajstić *et al.* 2007). Low pH and rapid burial were important factors in the preservation of the muscle tissues but recent research on invertebrate taxa from the Gogo Formation has shown that the action of sulfur-reducing bacteria prior to burial was also significant in the mineralisation of soft tissues (Melendez *et al.* 2013). In some instances individual cells are replicated by a single crystal of apatite, exactly replicating the structure of muscle and nerve fibres (Trinajstić *et al.* 2007). The recognition that mineralised soft tissues were present in the fossils (vertebrate and invertebrate) from Gogo led to different preparation techniques, reduced concentrations of acid and virtual preparation through synchrotron scanning. Using these techniques nearly all the postcranial musculature in the arthrodire *Compagopiscis croucheri* and the nuchal gap muscles in *Incisoscutum ritchiei* and *Eastmanosteus calliaspis* (Figure 3M₁-M₂) have been identified (Trinajstić *et al.* 2013). The significance of this discovery was that more muscles were found to be present in the neck than originally predicted from studies based on comparative morphology. Although the presence of paired head elevator and depressor muscles was predicted based on functional consideration, the division of the head elevators into medial and lateral muscles had not (Trinajstić *et al.* 2013). In addition, the presence of the cucullaris muscle, a head depressor muscle presumed to be common to all jawed vertebrates, was confirmed for the first time. A second group of specialised muscles, which had never been predicted, was found to be present in the ventral body wall (Trinajstić *et al.* 2013). Although their function is yet to be determined, their position at the junction of the trunk armour and the tail suggests that they play a role in minimising shear during tail propulsion (Trinajstić *et al.* 2013).

Although sexual dimorphism had been recognised in ptyctodonts (Watson 1934, 1938), it was not until the identification of claspers in the ptyctodontid *Ctenurella* (Ørvig 1960) that the possibility of internal fertilisation in ptyctodonts was suggested (Patterson (1965). In a review of the Scottish ptyctodont *Rhamphodopsis*, Miles (1967), noted it was impossible at that time to determine whether the mode of copulation in ptyctodonts resulted in oviparity or viviparity. This conundrum was finally solved when a single embryo (Figure 4A) was discovered in the ptyctodontid *Materpiscis attenboroughi*, which demonstrated beyond doubt the presence of internal fertilisation with live birth almost 200 million years earlier in the fossil record than previously known (Long *et al.* 2008; Trinajstić *et al.* 2012). One of the most crucial pieces of evidence in the determination of embryos in placoderms was the presence of the mineralised umbilical cord (Figure 4A) in *M. attenboroughi* (Long *et al.*

2008). Following this discovery, three embryos, previously identified as scales, were recorded from *Austroptyctodus gardineri* (Figure 4B) (Long *et al.* 2008). Male claspers had previously been identified by Miles & Young (1977) in *Austroptyctodus* (Figure 4C). Small dermal plates had also been recovered from the abdominal area of an arthrodire *I. ritchiei* (Figure 4D, E), but the absence of any evidence for sexual dimorphism and the honeycomb nature of the bone, which was

originally interpreted as being the result of digestion, meant that these plates were identified as prey items (Dennis & Miles 1981). Comparison with the honeycomb nature of the embryonic plates in the ptyctodonts (Figure 4F) allowed the reinterpretation of the arthrodire plates as embryonic bones (Long *et al.* 2009). The presence of an articulation surface on the pelvic girdle of *Austroptyllolepis*, interpreted as for claspers (Long *et al.* 2009), suggested that sexual dimorphism also occurred

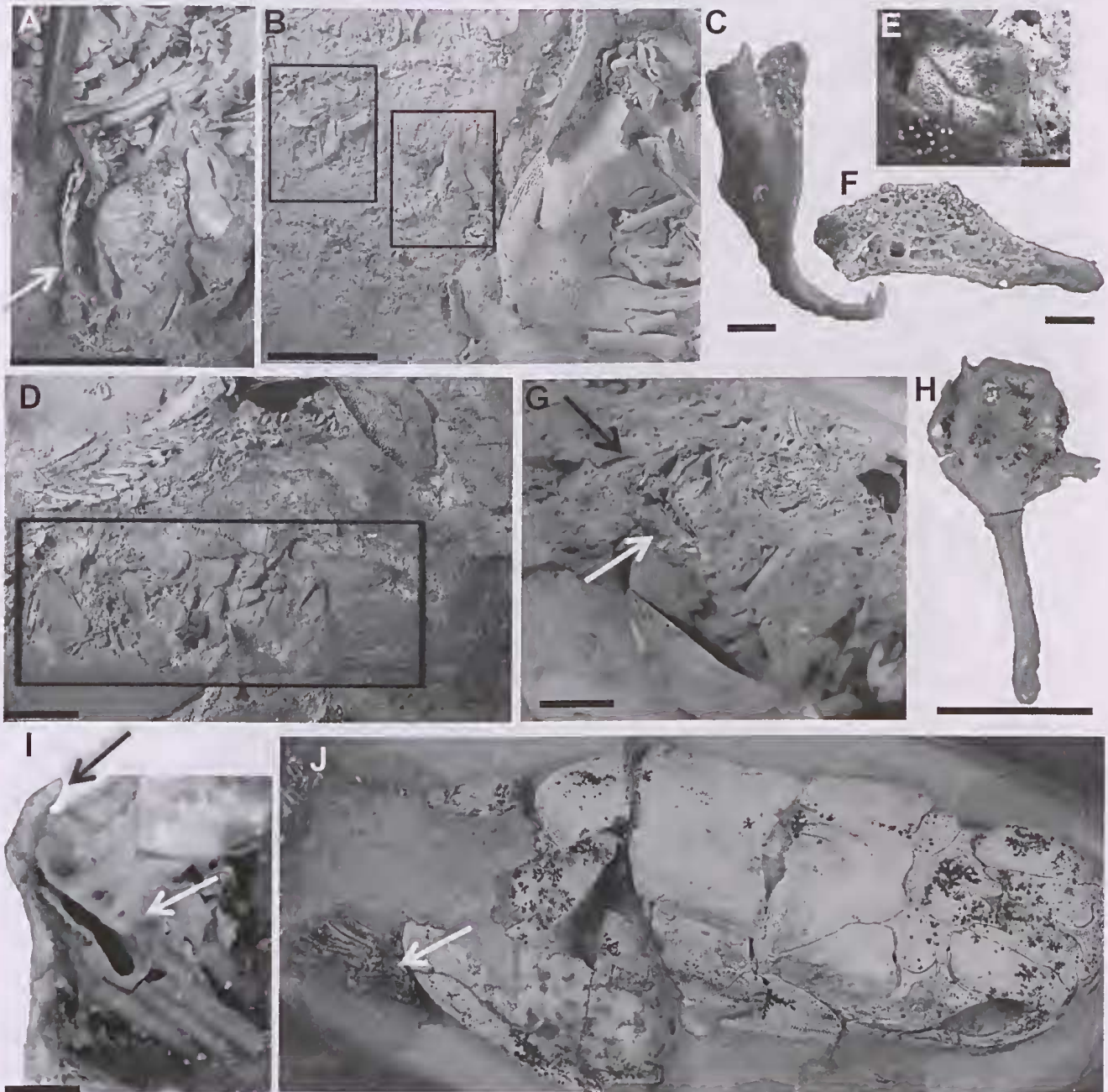


Figure 4 Reproductive structure in placoderms from the Gogo Formation. (A) *Materpiscis* embryo with detail of the mineralised umbilical cord indicated by a white arrow. (B) *Austroptyctodus gardineri*, internal view with 2 embryos within the rectangular outline. (C) Male clasper from *Austroptyctodus gardineri*. (D) Internal view of *Incisoscutum ritchiei* with embryonic bones within the rectangular outline. (E) Close up of embryonic plate from *Incisoscutum ritchiei*. (F) Embryonic plate from *Austroptyctodus gardineri*. (G) Internal view of *Incisoscutum ritchiei* showing male clasper (black arrow) and pelvic girdle (white arrow). (H) Detail of male clasper from *Incisoscutum ritchiei*; (I) close up of male clasper (black arrow) and pelvic girdle (white arrow) in *Incisoscutum ritchiei*. (J) Female specimen of *Compagopiscis croucheri* showing the pelvic girdle (white arrow). Scale bar: 1 cm in A, B, D, G, H, J; 1 mm in C, F; 2 mm in E; 5 mm in I.

in arthrodires. The final piece of the puzzle was revealed with the discovery of a male clasper (Figure 4G–I) in *I. ritchiei* (Ahlberg *et al.* 2009), which could be distinguished from the pelvic girdle (Figure 4G, I, J) and in *Holonema westolli* (Figure 5A, B) confirming sexual dimorphism with viviparity in ptyctodont and arthrodire placoderms (Trinajstic *et al.* in press a).

Soft tissues have also been recovered in the first and only acanthodian, *Halimacanthodes ahlbergi* described from the Gogo Formation (Burrow *et al.* 2012). The body outline is preserved in the resin-embedded side of the nodule, and was therefore protected during acetic acid preparation. The specimen represents a juvenile, as there is no scale cover in the mid-body region of the fish and there are a low number of growth zones in the scales. These features have been recognised as indicating a juvenile stage from comparison with the ontogenetic series in *Lodeacanthus gaujicus* (Upeniece 1996) from the Frasnian Lode Quarry, Latvia. The Gogo acanthodian shows a close affinity to *Howittacanthus kentoni* from the Frasnian lacustrine mudstones of Mt Howitt, Victoria (Long 1986).

The palaeoniscoid actinopterygians or ray-finned fishes have been revised in recent years by Choo *et al.* (2009) and Choo (2011), who have extended the actinopterygian faunal list of the site to five taxa, from the original two described by Gardiner (1984). The Gogo actinopterygians also show preserved soft tissues (Figure 5C) and, in rare cases, organs including the gut, gill area and liver (Trinajstic *et al.* in press b). The anatomical positions of these organs are comparable to those of extant actinopterygians. The path of the intestine is identified, as the cavity where the intestine ran has been infilled with calcite cement. Although this sort of replacement precludes preservation of gut contents (Trinajstic *et al.* in press b), conodont animals recovered from within the abdominal cavity (Nicoll 1977) and the branchial region (Figure 5D) of two specimens indicate that these fish were carnivores, consistent with the diet indicated by their dentition (Choo *et al.* 2009).

Most recent work on Gogo lungfishes includes description of new taxa of holodontid lungfishes including *Xeradipterus* (Clement & Long 2010) plus a new species of rhinodipterid, *Rhinodipterus kimberleyensis* (Clement 2012). Clement & Long (2010) also reported the first record of a marine lungfish showing air-breathing adaptations based on a specimen of *Rhinodipterus* from the Gogo Formation with cranial rib articulations on its braincase.

The tetrapodomorph fish *Gogonassus andrewsae* (Long 1985) is now known from several relatively complete specimens (Holland & Long 2009) (Figure 3A). Holland (2013) has recently described the pectoral girdle and fin in detail. Large holes on top of the head are identified as spiracles in this genus and were suggested as accessory breathing structures by Long *et al.* (2006). Recent work on the physiology of the modern air-breathing fish *Polypterus* now confirms that spiracular breathing was common in basal osteichthyans and most likely explains why fish like *Gogonassus* have such large spiracles (Graham *et al.* 2014).

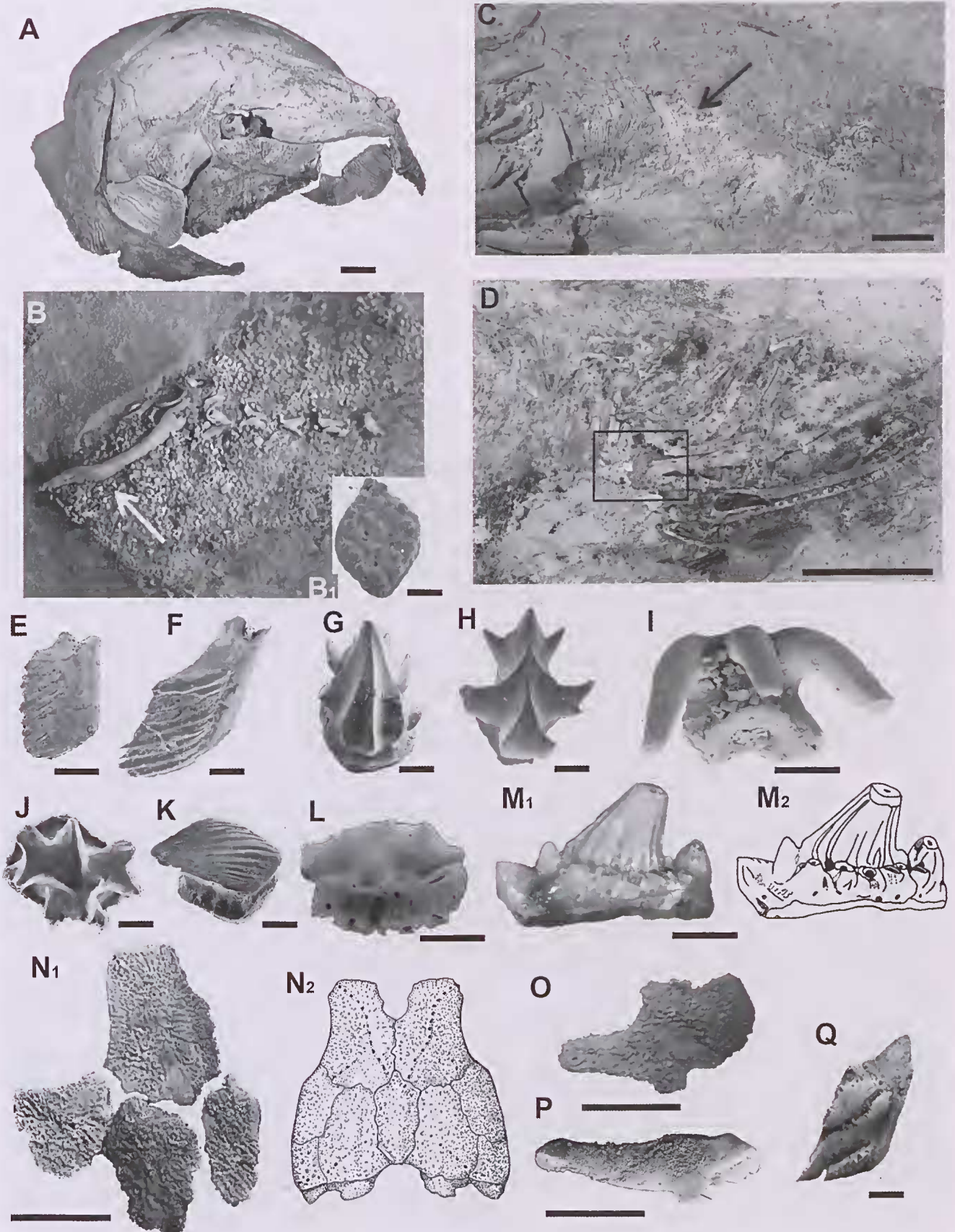
The other important aspect of the exceptional preservation from the Gogo Formation has been the ability to identify and compare isolated scales from the contemporaneous Gneudna Formation, Carnarvon Basin (see below) and the Virgin Hills Formation, Canning Basin. The variation in scale morphology present in palaeoniscoids is exhibited in key features including shape and ornamentation, enabling identification of the body area from which isolated scales originated. Following Esin (1990), different squamation areas in the Gogo palaeoniscoids have been recognised, enabling two species, *Moythomasia durgaringa* and *Mimia toombsi* to be identified from the Gneudna Formation (Figure 5E, F) (Trinajstic 1999c, 2000) and scales from *M. durgaringa* to be identified from the Virgin Hills Formation (Trinajstic & George 2009) and Hull Range (Chow *et al.* 2013), Canning Basin, providing biostratigraphic constraints for these strata. In addition scales from the placoderm *Holonema westolli* Miles 1971 (Figure 5B) were also identified in the Gneudna Formation (Figure 5B₁) based on the description of a complete tail recovered from the Gogo Formation (Trinajstic 1999a).

As noted above, the Gogo Formation fishes are further contributing important information on reproduction in early jawed fishes, including viviparity as an early vertebrate reproductive strategy, multiple embryos and ontogenetic series, which enable questions of taxonomy, phylogeny and development to be addressed (Johanson & Trinajstic 2014, Trinajstic *et al.* in press b).

VIRGIN HILLS FORMATION: FRASNIAN

The microvertebrate fauna described from a measured section at Horse Spring in the Canning Basin is dominated by thelodont scales (Figure 5G, H) and phoebodont teeth (Figure 5I) with a smaller number of acanthodian and palaeoniscoid scales as well as protacrodont teeth also recovered (Turner 1997; Trinajstic

Figure 5 Vertebrate remains from the Gogo, Virgin Hills and Gneudna Formations. (A) Head shield of *Holonema westolli*. (B) Body scales and clasper (white arrow) *Holonema westolli* from the Gogo Formation; (B₁) body scale of *Holonema westolli* from the Gneudna Formation. (C) *Moythomasia durgaringa* in lateral and internal view showing mineralised soft tissue (white arrow). (D) *Gogosardinia* with conodont (rectangular outline) in the branchial regions. (E) *Moythomasia durgaringa* type A scale and (F) type B scale from the Gneudna Formation. (G, H) Scales from *Australolepis seddoni* in crown view Virgin Hills Formation, Horse Spring, Canning Basin. (I) *Phoebodus bifurcatus* tooth in crown view Virgin Hills Formation, Horse Spring, Canning Basin. (J) Scale from *Australolepis seddoni* in crown view, Gneudna Formation. (K) *Cheiracanthus* sp. body scale in crown view. (L) *Phoebodus* sp. tooth in crown view, Gneudna Formation. (M₁) *Emerikodus* tooth in lingual view from the Gneudna Formation; (M₂) line drawing of *Emerikodus*. (N₁) Head shield plates of *Kimbrynaodus* from the Gneudna Formation; (N₂) line drawing of reconstruction of the head shield of *Kimbrynaodus*. (O) Marginal plate in lateral view of *Kimbrynaodus* from the Gneudna Formation. (P) Lower tooth plate of *Kimbrynaodus* from the Gneudna Formation. (Q) Palaeoniscoid scale *Gogosardinia coatesi* in crown view from the Gneudna Formation. Scale bar: 2 cm in A; 1 mm in B, F–M, Q; 2 mm in E; 1 cm in O, N; 5 mm in P.



2000; Trinajstić & George 2009). The discovery by Trinajstić (2000) represented the first record of the thelodont *Australolepis seddoni* (Figure 5G, H) co-occurring with conodonts and extended the known stratigraphic range to as young as the standard Montagne Noire conodont zone 10 (CZ10 MN) (Trinajstić & George 2009). This thelodont is a useful index fossil that defines the early Frasnian in East Gondwana (Turner 1997). The presence of *A. seddoni* scales in the Hull Range has confirmed the Frasnian age of back-reef facies, which are difficult to date with conodonts and ammonoids (Chow *et al.* 2013). The biogeographic range of *A. seddoni* is now known to have extended westwards along the northern margin of Gondwana with new discoveries in Iran and possibly Poland (Turner *et al.* 2002; Hairapetian *et al.* in press).

Numerous small acanthodian scales have also been recovered from the lower beds of the Horse Spring section and their generic morphology and lack of ornament led to them to be placed in open nomenclature (Trinajstić & George 2009). Following the description of *Halimacanthodes ahlbergi* the scales from Horse Spring have now tentatively been referred to this taxon (Burrow *et al.* 2012). Smooth-crowned acanthodiform scales are common components in Frasnian strata (Burrow *et al.* 2010). Other taxa that co-occur in the Virgin Hills and Gogo formations are scales attributed to the palaeoniscoid *Moythomasia durgaringa* and toothplates from the lungfish *Chirodopterus australis*.

Teeth of phoebodont sharks (Figure 5I) have also been recovered from the Horse Spring section (Trinajstić & George 2009) and can be correlated with the standard phoebodont zonations elsewhere in Australia and worldwide (Young & Turner 2000, Ginter *et al.* 2010). Although known to have a global (at least Paleotethyan) range, phoebodont taxa had not been recorded in Western Australia until their recovery from conodont residues at Horse Spring (Trinajstić & George 2009). Phoebodonts have proved useful for biostratigraphy in Givetian to Famennian strata (Ginter *et al.* 2010) and their range into the Famennian has recently been reported in Western Australia (Roelofs *et al.* 2013).

NAPIER FORMATION: FRASNIAN

Long (1988) recorded a large upper toothplate (supragnathal) of a ptyctodontid placoderm identified as *cf. Campbellodus* sp. from the Napier Formation in the Canning Basin. In addition, a microvertebrate fauna including scales from thelodonts, acanthodians, chondrichthyans and actinopterygians, and teeth from at least three species of stethacanthid and cladodont sharks have been recovered from beds throughout the section at South Oscar Range.

NAPIER FORMATION: FAMENNIAN

One of the earliest records of Famennian aged vertebrate material in the Canning Basin is from Barker Gorge, in the Napier Range. The fossil was collected by H P Woodward in 1906 and identified as: '...a large Devonian fish (new to science) allied to *Coccosteus*' by his father Henry Woodward, then Keeper of Geology at the British Museum (Glauert 1910 p. 112). A Smith Woodward, who took over as Keeper from Henry Woodward (no relation) in 1901, agreed writing: 'The Western Australian Fossil

looks remarkably like a piece of a large Devonian Coccosteian, hitherto unknown in the Australian Region' (Glauert 1910 p. 113). Etheridge (1918) described (but did not figure) similar material collected in 1916 by H Basedow from 'near Old Napier Downs homestead' as the stromatoporoid *Stromatoporella kimberleyensis*. During a study of the stromatoporoids from the reef complexes, Cockbain (1976) re-examined the Woodward and Basedow material and concluded that it was not a stromatoporoid: additional testing including thin sectioning and X-ray diffraction analyses confirmed the original identification as arthrodire bone (R S Miles in Cockbain 1976). The recovery of further vertebrate fossils from the area has been scant, with a single shark tooth *Stethacanthus cf. thomasi* recovered from mineral drillcore (NRD103) at Napier Range and a single tooth of *Thrinacosodus ferox* recovered from Napier Range 1 well located east of Chedder Cliffs and dated as Late Famennian (Chow *et al.* 2004), based on the associated conodont fauna. Vertebrate remains have been recovered in outcrop from Chedder Cliffs, although, with the exception of some incomplete placoderm dermal plates, most are so broken they are impossible to identify. Conodont samples from Barker River have yielded a single phoebodont tooth and some isolated 'ctenacanthid' type scales.

VIRGIN HILLS FORMATION: FAMENNIAN

A single large placoderm, *Westralichtlys*, was recovered from the *crepida* zone of the Virgin Hills Formation by Curt Teichert and this was subsequently prepared and described by Long (1987). In 2009, Peter Haines identified bone from a large placoderm in a measured section at Casey Falls, from close to where the original specimen was thought to have been recovered. The new specimen was excavated from the rock in 2011 and is currently undergoing preparation. The plates represent the trunk armor of a large dinichthyid and have been tentatively identified as belonging to *Westralichtlys*, but they await formal description. Towards the top of the section there is a breccia where large isolated, but broken, placoderm plates are present. It has not been possible to identify these fragmentary remains but as they occur in a horizon above strata dated by conodonts as mid-Famennian, this confirms a Famennian age for the uppermost beds. Placoderms did not survive the end-Famennian extinction event, and therefore a younger Carboniferous age for the upper part of the section measured at Casey Falls is ruled out.

The measured section at the Casey Falls locality yielded few microvertebrates, mostly shark teeth, with a small number of acanthodian and palaeoniscoid scales. Preliminary work on the shark fauna confirms the presence of phoebodonts, as elsewhere in Australia (Turner 1982b, 1993; Young & Turner 2000). The ramp facies, above the Casey Falls section, is dominated by a diverse shark assemblage, which includes teeth from protacrodontids, stethacanthids, lonchidiids and the phoebodont *Thrinacosodus tranquillus*. Numerous palaeoniscoid scales and teeth and lower numbers acanthodian, scales are also present.

Interestingly, thelodonts, phoebodonts and porolepiforms are yet to be recorded from the Gogo Formation, even though these taxa are known from the

Frasnian and Famennian Virgin Hills and Napier formations in the Canning Basin. This is probably a reflection of the preferred environments of these fish, with thelodonts typically in shallower marine, marginal marine to freshwater settings (Turner 1997). Phoebeodont sharks, apart from one thrinacrodont from the late Mississippian of the USA, are only known from isolated teeth but typically occur in marine rocks (Ginter & Turner 2010).

Carboniferous

There is a major environmental change towards the end of the Famennian with the cessation of reef building; the marine habitats of the Carboniferous period are dominated by carbonate ramps. The end Famennian is also marked by a major extinction event that affected vertebrates and marked the demise of the placoderms (although the number of families was already reduced after the Frasnian/Famennian extinction event) and a major radiation of sharks and actinopterygians, which is reflected in the shallow-water facies of the Laurel Formation in the Canning Basin. Palaeoniscoid remains (teeth, scales and radial bones) and acanthodian scales

dominate the fossiliferous units. Turner (1982a) identified *Thrinacodus ferox* from Oscar Hill and renamed earlier Lower Carboniferous shark material described by Thomas (1957). Edwards (1997) found teeth of a new *Thrinacodus* sp. from a trench dug across the Upper Devonian–Lower Carboniferous by Mawson *et al.* (1988) to obtain conodont data; Ginter & Sun (2007) named this taxon *Thrinacodus bicuspidatus* and its range is within the basal Tournaisian in China and Western Australia. Recent work (Roelofs *et al.* 2013) has also uncovered shark teeth, scales and spines from 21 different taxa including *Ageleodus* sp., *Thrinacodus ferox* (Figure 6A), *Stethacanthus* spp., *Protacrodus* spp., (Figure 6B, E), *Deihim mansureae*, *Cassisodus* sp., *Helodus* spp., *Lissodus* spp. (Figure 6C, D), *Orodus* sp. and a ctenacanthid sp. (Figure 6F). A partial tooth from a large stethacanthid shark is also of note as it bears strong affinities to teeth in a fragmented but 3D preserved partial jaw and palate from a large specimen of *Stethacanthus* sp. from the Bonaparte Basin (Turner 1991; Turner *in* Jones *et al.* 2000; Turner *et al.* 1994; Burrow *et al.* 2010). This indicates the presence of large predatory sharks early in the Carboniferous across north Western Australia (Burrow *et al.* 2010).

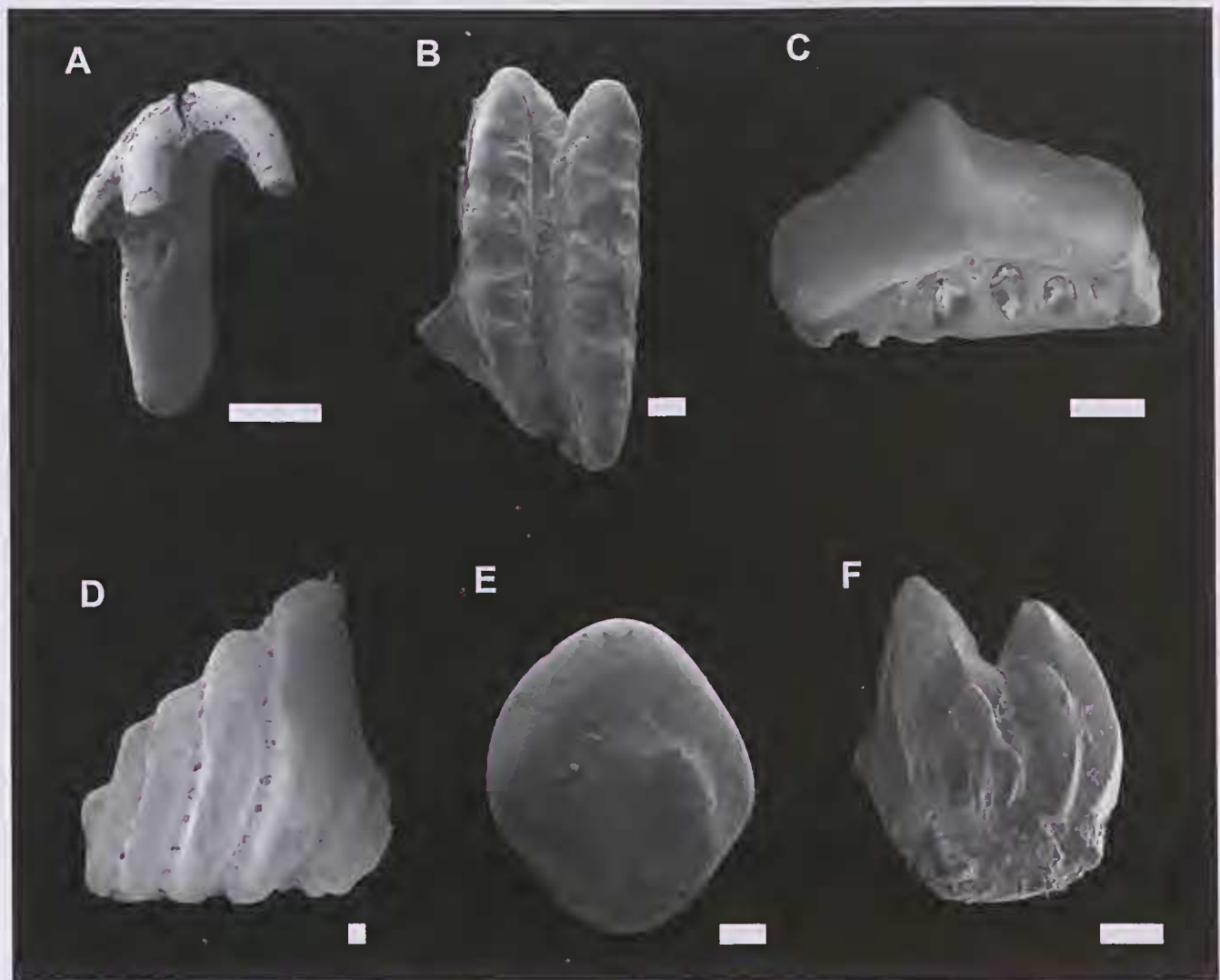


Figure 6 Carboniferous microremains from the Laurel Formation, Canning Basin. (A) *Thrinacodus ferox* tooth in crown view. (B) Partial *Protacrodus* sp. tooth whorl in crown view. (C) *Lissodus* sp. tooth in lingual view. (D) *Lissodus* sp. tooth whorl in crown view. (E) *Protacrodus* sp. scale in basal view. (F) Ctenacanthid scale in crown view. Scale bar: 0.4 mm.

Further work on the diverse shark fauna of the Viséan Utting Calcarenite, Weaber Group, of the Bonaparte Basin has brought to light at least 18 different taxa of eugeneodontid and other sharks as well as sarcopterygian and actinopterygian remains (Chambers 2003; Burrow *et al.* 2010).

Carnarvon Basin

Fish fossils are mostly known only from Late Devonian sediments in the Carnarvon Basin. The early Frasnian Gneudna Formation is interpreted as being deposited along a shallow marine shelf (Hocking *et al.* 1987). Conformably overlying and interfingering with the Gneudna Formation is the Munabia Sandstone where deposition was initially in a tidal environment grading up to a braided-fluvial system (Moors 1981) with conodonts indicative of marine incursion in the upper part of the section (Nicoll 1979; Hocking *et al.* 1987). The Frasnian/Famennian boundary occurs within the Munabia Sandstone and the upper part of the section grades into the Famennian Willaraddie Formation, which is at least partly laterally equivalent (Gorter *et al.* 1998). During the latest Devonian and into the Tournaisian a shallow sea transgressed across the region, reflected by the deposition of the Moogooree Limestone (Hocking 1990). The Permian Byro Group represents cold-water facies, predominantly comprising black shale deposited under anoxic conditions in the outer offshore zone and a lighter coloured shale deposited under less-restricted conditions in the inner offshore zone (Hocking *et al.* 1987). The changes in bathymetry are thought to reflect tectonic events related to the breakup of Gondwana (Hocking *et al.* 1987).

Vertebrate fossils of the Carnarvon Basin

Devonian

FRASNIAN

The Gneudna Formation is laterally discontinuous, with most paleontological studies (vertebrate and invertebrate) having been concentrated on the type section. The Gneudna type section was described as depauperate in fossil taxa (Dring 1990), however, this statement is only accurate for the invertebrates: the fish fauna is now known to be one of the most diverse marine vertebrate assemblages of this age, with nearly 20 taxa present, the majority of which are represented as microfossils (Turner & Dring 1981; Trinajstić 1999a, b, c; Long & Trinajstić 2000; Trinajstić 2001a, b; Trinajstić & George 2009).

George Seddon (1969) discovered the first vertebrate fossils in conodont residues and determined the remains as either teeth or scales belonging to fish species. Dring (1980) recovered additional fish remains and recorded the presence of placoderms, palaeoniscoids, acanthodians and lungfish; only the thelodonts were formally described following Turner's identification of some of Seddon and Dring's scales, formally described as *Australolepis seddoni* by Turner & Dring (1981). This was the first evidence of the thelodonts surviving the Givetian/Frasnian extinction event and into the Late Devonian and at the time represented the youngest occurrence of thelodonts in the world. Scales of *A. seddoni*

(Figure 5J) have been used by Turner (1997) to define the early–mid-Frasnian zone in East Gondwana. So far this species is confirmed from Frasnian deposits CZ 4–10 of the Gneudna and Virgin Hills formations, Western Australia (Trinajstić & George 2009) and eastern Iran (Gholamalalian *et al.* 2010).

Following these discoveries, a rich microvertebrate fauna was described that includes additional scales types from *Australolepis seddoni*, tail scales from the arthrodire *Holonema westolli* (Figure 5B₁), body scales from the palaeoniscoids *Minia gardineri* (Figure 5E) and *Moythomasia durgarunga* (Figure 5F), acanthodian scales recently identified as coming from *Homalacanthus ahilbergi* and *Cheiracanthus* sp. (Figure 5K), toothplates from the lungfish *Chirodipterus australis*, porolepiform scales, phoebodont teeth (Figure 5L), and a new genus of shark *Emerikodus* (Figure 5M₁, M₂). At the time of these descriptions (Trinajstić 2000) the vertebrate fauna was considered far more diverse than that recovered from the Gogo Formation because shark, acanthodian and coelacanths had not yet been discovered in it (Long & Trinajstić 2010). As noted, thelodonts, phoebodonts and porolepiforms are yet to be recorded from the Gogo Formation although these taxa are known from the Frasnian and Famennian Virgin Hills and Napier Formations in the Canning Basin.

In addition to the microvertebrates a small number of macrovertebrates have also been found, with placoderm remains the most common. An anterior dorsolateral plate (WAM 91.4.35), part of the shoulder armour, attributed to the actinolepid placoderm *Groenlandaspis* sp. was identified by Long (1993). *Groenlandaspis* occurs in the Early–Middle Devonian *Wullagoonaspis* fauna in central New South Wales and the Toomba Range southern Queensland (Ritchie 1973, 1975; Young 1993; Young & Goujet 2003), and right through the Middle and Late Devonian successions throughout Australia. Although common in purported freshwater facies of this age and yet known to have a global occurrence, *Groenlandaspis* has not been reported from the Gogo Formation (Long & Trinajstić 2010).

Other placoderm material comprises plates from the trunk armour and includes a right mesial lateral 2 plate, an anterior ventrolateral plate and an anterior dorsolateral plate of *Boltriolepis* and a head shield plate (nuchal plate) from the arthrodire *Holonema westolli*. The most complete placoderm remains are from the ptyctodont *Kimbryanodus* described by Trinajstić & Long (2009) (Figure 5N₁, P). The holotype comprises the dermal plates that make up the shoulder girdle and represent the only articulated remains recovered. However, one bed, in the lower part of the section, contains a large number of isolated, but associated plates, including a complete set of dermal head (Figure 5N₁, N₂) and trunk shield plates and some endochondral elements of the braincase (Trinajstić & Long 2009). This ptyctodont is one of four species known from Western Australia, the other three occurring in the Gogo Formation. A phylogenetic analysis (Trinajstić & Long 2009) places this taxon as closely related to *Materpiscis* and *Austroptyctodus*, both endemic to the Gogo Formation.

Long (1985) referred the lungfish, originally ascribed by Seddon (1969) to *Dipterus* cf. *digitatus*, to *Chirodipterus*

australis. Many new specimens of isolated lungfish toothplates have been found throughout the section and one partial dipnoan braincase from near the top of the section. Comparisons with the Gogo osteolepiform *Gogonaspis andrewsae* (Long 1985, name amended) show that the Gneudna specimens are significantly larger. Large sigmoid-shaped symphyseal teeth and a nearly complete dentary lined with large conical teeth suggest affinity with the genus *Onychodus*, in particular to *Onychodus jaudemarrai* from Gogo Formation (Andrews *et al.* 2006), although the Gneudna species is much larger with more robust teeth (Long & Trinajstić 2000). Isolated rounded scales with regions of small upturned flat tubercles have been referred to an indeterminate porolepiform, with the scales somewhat similar to those of *Glyptolepis* sp. (Jarvik 1980 figure 178).

The dipnoan genera *Chirodipterus* and *Adololopas*, as well as the placoderms *Bothriolepis* and *Holonema*, are found in the top of the section, which lies in the *falsiovalis* conodont zone and has been dated as lower Frasnian. *Holonema* is represented both in the Gneudna and the Gogo Formations by the species *H. westolli* (Trinajstić 1999a). The palaeoniscoid species, including scales attributed to juvenile specimens, recorded from the Gneudna and Gogo Formations are *Moylthomasia durgaringa* (Trinajstić 1997b, 1999a, b) and *Minia toombsi* (Trinajstić 1999c), both species occurring throughout the section. Choo *et al.* (2009) described three additional palaeoniscoid taxa from the Gogo Formation. One of these, *Gogosardina coatesi*, has scales with linear ornament, which indicates that the juvenile scales from the Gneudna Formation (Trinajstić 1999b) were misidentified and thus need to be attributed to *Gogosardiina coatesi* (Figure 5Q).

FRASNIAN–FAMENNIAN

A scant macrovertebrate fauna including remains of *Bothriolepis* sp., *Holonema* sp. and indeterminate scales of an osteolepiform sarcopterygian was collected from the lowermost outcrops of the Munabia Sandstone and described by Long (1991). These fossils constitute the only record of macrovertebrates from this horizon; however, collecting and processing by CJB in 2011 revealed a similar microvertebrate fauna to the underlying Gneudna Formation. Long (1991) attributed the fauna to a likely Frasnian age based on the similarities in shape and dermal ornament of the Munabia *Holonema* anterior median ventral plate to the Gogo *Holonema westolli* plates.

FAMENNIAN

As with the Canning Basin, vertebrate fossils are rare in Famennian strata of the Carnarvon Basin. Within the Willaraddie Sandstone, John Long in 1995 first collected placoderm remains preserved as natural impressions including plates from *Bothriolepis* and a phyllolepid posterior ventrolateral plate. Recently in 2011, Eva Papp (ANU) collected additional phyllolepid plates but these are undiagnostic. Phyllolepids are widespread in the Givetian and younger rocks in Gondwana (around Australia, Antarctica, Turkey, Venezuela) but do not occur until the Late Devonian (Famennian) in the Northern Hemisphere (Europe, Russia, Greenland, North America) following the post-Givetian Laurentia–North

Gondwana collision and thus a Gondwanan origin for the group was proposed by Young (2005).

Carboniferous

The Moogooree Limestone has yielded a rich microvertebrate fauna that has yet to be formally described, although there is a preliminary report (Trinajstić & George 2007). Abundant actinopterygian (palaeoniscoid teeth, radial bones, and scales: Figure 7A) and acanthodian (scales: Figure 7B) remains have been recovered. The chondrichthyan taxa show great diversity with representatives of the Phoeodontidae (*Thrinacodus ferox*, *Thrinacodus bicuspidatus* Figure 7C), Protacrodontidae (*Deihim mansureae* Figure 7D–E, *Protacrodus* sp.), Stethacanthidae (*Stethacanthus* sp. Figure 7F), Ctenacanthidae (scales) and Helodontidae (*Helodus* sp.) present. The diverse shark assemblage shows strong affinities with the Canning Basin shark fauna as well as with faunas from Queensland (Turner 1990; Burrow *et al.* 2010), South China (Wang & Turner 1995; Ginter & Sun 2007), Morocco (Derycke *et al.* 2008) and Iran (Hairapetian & Ginter 2009).

Permian

In contrast to eastern Australia (Turner 1993), the Permian record of fossil fishes in Western Australia is sparse, with chondrichthyans the only taxon so far represented. The first shark tooth to be recognised from Permian strata in the Carnarvon Basin comprises 15 teeth arranged along a common spiral root and was designated as *Edestus davisii* by Woodward (1886). The specimen was collected in the valley of the Arthur River, although as the tooth whorl was not found *in situ* its exact locality could not be determined. The discovery represented the first record of a novel group of chondrichthyans characterised by the presence of a continuous spiraled tooth whorl. The first description of this unique shark was of *Helicoprion bessonowi* from the Ural Mountains by Karpinsky (1899) and in his monograph he referred the tooth recovered by Woodward to his new genus *Helicoprion*. However, Eastman (1902) referred the Western Australian tooth whorl to the genus *Campyloprion*, which he had erected, and Hay (1909) referred the material to another genus *Lissoprion*. Controversy remained as to the exact taxonomic affinities of the Western Australian tooth whorl until in 1937 a second specimen comprising 5 teeth was recovered from the bed of the Minilya River near Wandagee Station, although, it too was not *in situ*. Two years later a third specimen was recovered *in situ* (Teichert 1940) from the Wandagee Stage (Teichert 1939) [now Wandagee Formation (Condon 1967)] and this new material confirmed the interpretation of Karpinsky (1912) that Woodward's original Western Australian tooth whorl belonged to the genus *Helicoprion*, and all three specimens were referred to *Helicoprion davisii* by Teichert (1940).

Helicoprion has a worldwide distribution and its importance in biostratigraphy and correlation was documented early (David & Süssmilch 1931). However, it is the unique morphology of the continuous spiraled tooth whorl and how it functioned that has intrigued scientists the most. Karpinsky (1899) variously reconstructed the spiral tooth whorl at the extreme

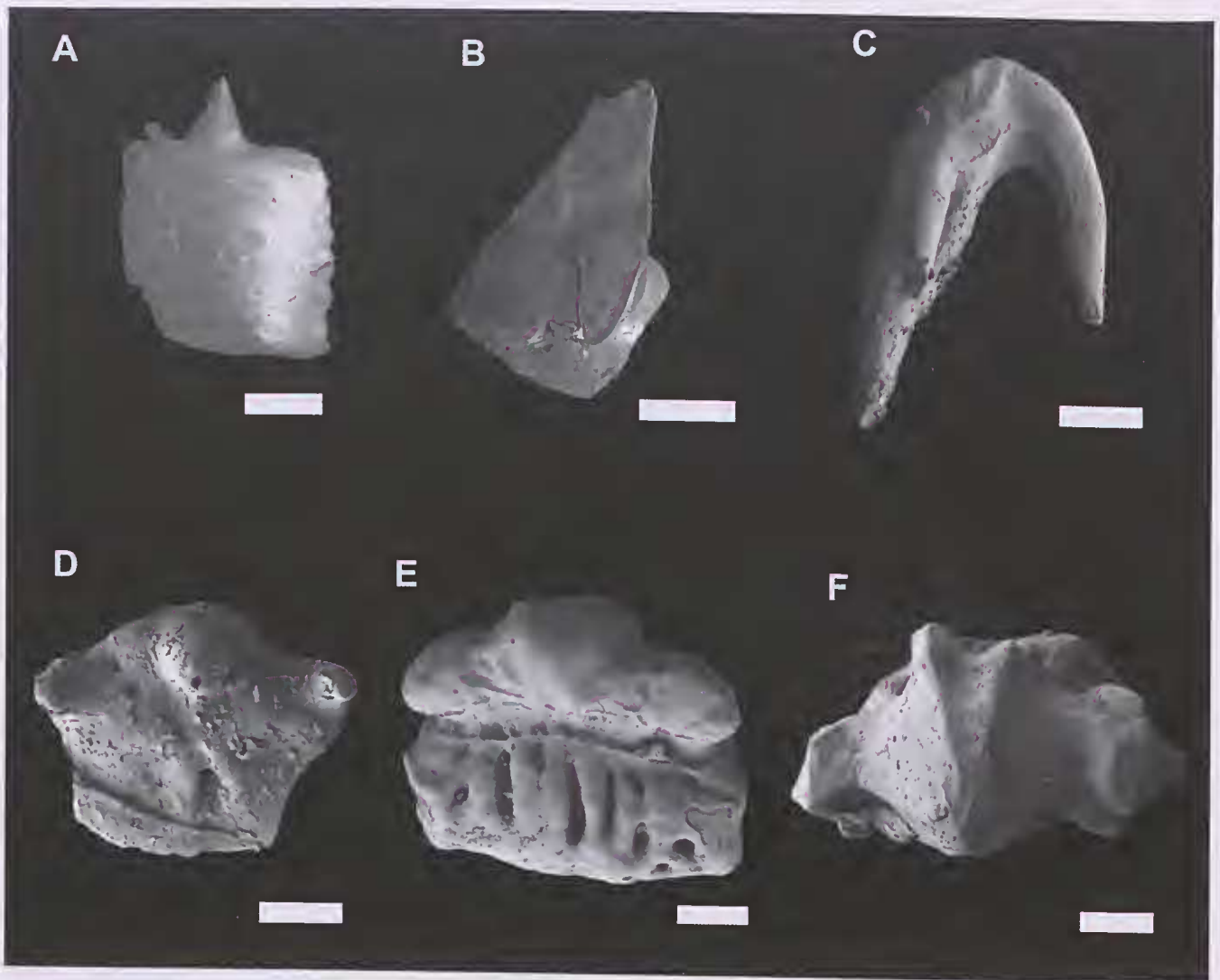


Figure 7 Carboniferous microremains from the Moogooree Formation, Carnarvon Basin. (A) Palaeoniscoid scale in crown view. (B) Acanthodian scale in crown view. (C) *Thrinacodus bicuspidatus* tooth in labial view. (D) Stethacanthid sp. Tooth in crown view. (E) *Deihim mansureae* tooth in lingual view. (F) *Deihim mansureae* tooth in labial view. Scale bar: 0.4 mm.

anterior of the upper mouth, on the leading edge of the dorsal fin and even on the tail, although most recent reconstructions show the tooth whorl overhanging the lower jaw (Long 1995). Computerised tomographic scans of the only *Helicoprion* specimen to preserve endoskeletal elements associated with the tooth whorl have revealed that it occupied the complete mandibular arch (Tapinila *et al.* 2013). The largest teeth on the tooth whorl were positioned at the back of the mouth and the shark is interpreted to have eaten soft prey such as squid, using a saw-like motion to slice prey (Tapinila *et al.* 2013).

BIOGEOGRAPHY

Ordovician

The distribution of arandaspid indicates interchange between Australia and South America via northern Gondwana with occurrences in Bolivia, Argentina and Oman as well as central and western Australia (Sansom *et al.* 2013), with all occurrences in a narrow environmental range in nearshore facies. The Larapinta

seaway must have been open between the latter two regions, at least intermittently in the Middle to Late Ordovician to allow dispersal from the Amadeus to the Canning Basin (Blewett 2012).

Silurian

The rare vertebrate faunas recovered from the Silurian of Western Australia show possible affinities with mid to Late Silurian assemblages from Iran, the Baltic and northern Eurasia, and possibly South China (Hairapetian *et al.* 2008; Burrow *et al.* 2010; Turner 2014), all in deposits that are also from shallow marine to evaporitic environments. The faunas differ markedly from those of a similar age in southeastern Australia (Burrow *et al.* 2010). Porosiform poracanthodid remains are found in several of the eastern Australian deposits, but are so far lacking from Western Australia. The only described thelodont known from eastern Australia is a purported turiniid, *Turinia fuscina* (Turner 1997). This form, however, is similar to that described as *Niurolepis susaunae* in Iran; for now it is best left as ?*Turinia fuscina* (Burrow *et al.* 2010). The new Western Australian thelodont(s)

resemble thelodontid and loganelliid taxa found elsewhere in northern Gondwana and parts of Laurentia; there are possible links also with rare thelodont scales found in Indonesia (Turner *et al.* 1995; Hairapetian & Ginter 2009).

Devonian

EMSIA

The key taxon of the Wilson Cliffs borehole assemblage, *Turinia australiensis* (Figure 1A–D), has an interesting transcontinental distribution. In southeastern Australia, all occurrences of *Turinia australiensis sensu stricto*, both marine and non-marine, are of late Pragian to early Emsian age (Turner 1997). Distribution of *T. australiensis* and closely related species extends westward from beds referred to the Cravens Peak Formation, western Queensland, from the Mulga Downs Group, Darling Basin, western New South Wales, and Mt Winter beds of the Pertnjarra Group, Amadeus Basin, central Australia (Young *et al.* 1987; Turner 1997), on to the type locality of Wilson Cliffs in the Canning Basin, and other boreholes in Western Australia (Burrow *et al.* 2010; Turner 2014). These records indicate periodic shallow-water marine incursions of the predominantly non-marine basins of central Australia, following the alignment of the older ephemeral Larapinta seaway.

FRASNIAN

The common vertebrate fauna in the three Paleozoic Basins of Western Australia supports tectonic data indicating a connection, via the North West Shelf, between the Carnarvon and Canning Basins (Stuckmeyer & Totterdell 1992). There are also greater faunal similarities between the marine faunas of Western Australia and those of northern and western Gondwana, consisting primarily of what are now South America, Africa, Iran and the Arabian Peninsula and Armorica than with the faunas of East Gondwana comprising eastern Australia, Antarctica and southeastern parts of China, a pattern similar to that seen with certain invertebrates (Feist & McNamara 2007, 2013; McNamara *et al.* 2009). This may reflect the fact that the vertebrate faunas of eastern Australia come from predominantly marginal/non-marine facies. However, an alternative hypothesis is that during the early Frasnian, eastern Australia was influenced by different ocean currents, which favoured migration to regions other than Western Australia. Klapper (1989) reported a similar pattern in the biogeographic relationship of conodonts, and concluded that migration of cosmopolitan species (both offshore and nearshore) was affected mainly by oceanic currents. A paleogeographic map indicating the main paleocurrents supports this view (Hairapetian *et al.* in press), with the coast of Western Australia influenced by different currents than the shores of what is now eastern Australia.

FAMENNIAN–CARBONIFEROUS

The Famennian is characterised by a more cosmopolitan vertebrate fauna (Young *et al.* 2010, Hairapetian *et al.* in press). This is reflected primarily in the occurrence of chondrichthyan taxa common to the Canning, Carnarvon and Bonaparte basins in Western Australia.

CONCLUSIONS

In general, studies over recent decades have increased the known biodiversity of Paleozoic vertebrate taxa from that part of Gondwana that is now Western Australia. Both new exploration and re-study of former drillcores and sites is yielding much new data, which is proving valuable in biostratigraphical studies and understanding of how this part of Gondwana was positioned at that time.

The significance of the macro- and microvertebrate faunas of Western Australia is their remarkable preservation, predominantly 3D, and in the majority of cases showing the fine histological details of the original hard tissues, without recrystallisation or other diagenetic processes obscuring their structure. The exception is the vertebrates from the Famennian Willaraddie Sandstone, where they are preserved as impressions, although 3D latex casts can be made of these. This has allowed significant breakthroughs in understanding of vertebrate faunas in Western Australia. The Gogo Formation area is also now noted as a rich and important contribution to Australian and global geoheritage (Long 2004, 2006; Turner 2009); the astonishing detail of preservation is grounds enough for putting this area forward for World Heritage status.

The recognition of variation in morphology, both ontogenetic and regional variation on articulated macrovertebrate fossils from the Gogo Formation, has made the identification of isolated scales to generic and, in some cases, to species level possible at other sites in Western Australia and globally. This has increased the known range of some taxa and also enabled the greater use of microvertebrate taxa for correlation, and phylogenetic, biostratigraphic and biogeographic studies.

ACKNOWLEDGEMENTS

We would like to thank several people for providing access to collections under their care: Peter Haines & Heidi Johnson (Geological Survey of Western Australia, Perth), Martha Richter (Natural History Museum, London), Mikael Siversson (Western Australian Museum) and David Pickering (Museum Victoria). Thanks to the reviewer Ken McNamara for helpful comments. This work is funded by Australian Research Council (ARC) QEII Fellowship to KT, ARC DP110101127 to KT, and JL, ARC DP 1092870 to KT, CB and JL.

REFERENCES

- AHLBERG P, TRINAJSTIĆ K, JOHANSON Z & LONG J 2009. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodirans. *Nature* 460, 888–889.
- ANDREWS M, LONG J, AHLBERG P, BARWICK R & CAMPBELL K 2006 (for 2005). The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Transactions of the Royal Society of Edinburgh Earth Sciences* 96, 197–307.
- BASDEN A, BURROW C J, HOCKING M, PARKES R & YOUNG G C 2000. Siluro-Devonian microvertebrates from south-eastern Australia. In: Blicek A & Turner S (eds) *Paleozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*, pp. 201–222. Courier Forschungsinstitut Senckenberg 223.

- BLEWETT R (Editor) 2012. *Shaping a Nation: a geology of Australia*. Geoscience Australia and ANU E Press, Canberra.
- BLIECK A & TURNER S 2000. IGCP 328: Palaeozoic microvertebrates final scientific report - Introduction. In: Blicke A & Turner S (eds) *Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*, pp. 1–67. Courier Forschungsinstitut Senckenberg 223.
- BLIECK A & TURNER S 2003. Global Ordovician vertebrate biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, 37–54.
- BURROW C J 2002. Lower Devonian acanthodian faunas and biostratigraphy of south-eastern Australia. *Memoirs of the Association of Australasian Palaeontologists* 27, 75–137.
- BURROW C J 2003. Redescription of the gnathostome fauna from the mid-Palaeozoic Silberband Formation, the Grampians, Victoria. *Alcheringa* 27, 37–49.
- BURROW C J, TRINAJSTIC K & LONG J 2012. First acanthodian from the Upper Devonian (Frasnian) Gogo Formation, Western Australia. *Historical Biology* 24, 349–357.
- BURROW C J, TURNER S & YOUNG G C 2010. Middle Palaeozoic microvertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld* 19, 37–54.
- CADMAN S J, PAIN L, VUCKOVIC V & LE POIDEVIN S R 1993. Canning Basin, W.A. *Bureau of Resource Sciences, Australian Petroleum Accumulations Report* 9.
- CHAMBERS B L 2003. Early Carboniferous vertebrate microfossils from the Bonaparte Basin, Northern Australia. MSc thesis, James Cook University, Townsville (unpubl) [not 2002 as in Burrow et al. 2010].
- CHOO B 2011. Revision of the actinopterygian genus *Mimipiscus* (= *Mimia*) from the Upper Devonian Gogo Formation of Western Australia and the interrelationships of the early Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 102, 71–104.
- CHOO B, LONG J A & TRINAJSTIC K 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. *Acta Zoologica* 90, 194–194.
- CHOW N, GEORGE A, TRINAJSTIC K & CHEN Z Q 2013. Stratal architecture and platform evolution of an early Frasnian syn-tectonic carbonate platform, Canning Basin, Australia. *Sedimentology* 60, 1583–1620.
- CLEMENT A 2012. A new species of long-snouted lungfish from the Late Devonian of Australia, and its functional and biogeographical implications. *Palaeontology* 55, 51–71.
- CLEMENT A & LONG J 2010. *Xerodipterus hatcheri*, a new dipnoan from the late Devonian (Frasnian) Gogo Formation, Western Australia, and other new holodontid material. *Journal of Vertebrate Paleontology* 30, 681–695.
- COCKBAIN A E 1976. *Stromatoporella kimberleyensis* Etheridge Jr. 1918 is a piece of bone. *Geological Survey of Western Australia Annual Report for 1975*, 133–135.
- CONDON M A 1967. The geology of the Carnarvon Basin, Western Australia. Part 2: Permian stratigraphy. *Bureau of Mineral Resources Bulletin* 77.
- DAVID T & SUSSMILCH C 1931. Upper Palaeozoic glaciation of Australia: *Geology Society of America Bulletin* 42, 481–522.
- DENNIS K & MILES R S 1981. A pachyosteorhynchid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society* 73, 213–258.
- DERYCKE C, SPALLETTA C, PERRI M C & CORRADINI C 2008. Famennian chondrichthyan microremains from Morocco and Sardinia. *Journal of Paleontology* 82, 984–995.
- DRING R 1980. Palaeobiology of the Gneudna Formation, Late Devonian (Frasnian), Carnarvon Basin, Western Australia. PhD thesis, University of Western Australia, Nedlands (unpubl.).
- EASTMAN C R 1902. On *Campyloprion*, a new form of *Edestus*-like dentition. *Geological Magazine* Dec. 4 v. 9, 148–152.
- EDWARDS A F 1997. Ichthyolith remains from the Devonian-Carboniferous Boundary of the Canning Basin, Western Australia. MSc thesis, Macquarie University, Sydney (unpubl.).
- ESIN D 1990. The scale cover of *Amblypterygia costata* (Eichwald) and the palaeoniscid taxonomy based on isolated scales. *Paleontological Journal* 2, 90–98.
- ETHERIDGE R JR 1918. Observations on Carboniferous and other fossils. In: Basedow H *Narrative of an expedition of exploration in northwestern Australia*, pp. 250–262. Royal Geographical Society of Australasia, South Australian Branch, Transactions 18.
- FEIST R & McNAMARA K J 2007. Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetian, Frasnian). *Geological Magazine* 144, 777–796.
- FEIST R & McNAMARA K J 2013. Patterns of evolution and extinction in proetid trilobites during the Late Devonian mass extinction event, Canning Basin, Western Australia. *Palaeontology* 56, 229–259.
- GAGNIER P-Y, BLIECK A, EMIG C C, SEMPERE T, VACHARD D & VANGUETAINE M 1996. New paleontological and geological data on the Ordovician and Silurian of Bolivia. *Journal of South American Earth Sciences* 9, 329–347.
- GARDINER B 1984. Relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum of Natural History (Geology)* 37, 173–428.
- GHOJAMALIAN H & KEBRIAEI M R 2008. Late Devonian conodonts from the Hojedk section, Kerman Province, Southeastern Iran. *Rivista Italiana di Paleontologia e Stratigrafia*, 114, 17–181.
- GINTER M, DUFFIN C & HAMPE O 2010. Chondrichthyes (Paleozoic Elasmobranchii: teeth). In: Schultze H-P (ed.) *Handbook of Paleichthyology*, vol. 3D. Friedrich Pfeil Verlag, München.
- GINTER M & IVANOV A 1992. Devonian phocodont shark teeth. *Acta Palaeontologica Polonica* 37, 55–75.
- GINTER M & SUN Y 2007. Chondrichthyan remains from the Lower Carboniferous of Muhua, southern China. *Acta Palaeontologica Polonica* 52, 705–727.
- GINTER M & TURNER S 2010. The Middle Palaeozoic selachian genus *Thrinacodus*. *Journal of Vertebrate Paleontology* 30, 1666–1672.
- GLAUERT L 1910. New fossils from Barker Gorge, Napier Range, Kimberley. *Geological Survey of Western Australia Bulletin* 36, 111–114.
- GORTER J, MORY A & NICOLL R 1998. Sequence stratigraphy and hydrocarbon potential of the Middle to Upper Devonian (Givetian–Frasnian) sequences in the Carnarvon Basin, Western Australia. In Purcell P C & Purcell R R (eds) *The sedimentary basins of Western Australia* 2, pp. 450–510. Petroleum Exploration Society of Australia Symposium, Perth, WA, 1998 Proceedings.
- GRAHAM J B, WEGNER N C, MILLER L A, JEW C J, LAI N-C, BERQUIST R M, FRANK L & LONG J A 2014. Spiracular air breathing in polypterid fishes and its implications for aerial respiration in stem tetrapods. *Nature Communications* 5, doi:10.1038/ncomms4022.
- GROSS W 1971. Unterdevonische Thelodontier- und Acanthodier-Schuppen aus Westaustralien. *Paläontologische Zeitschrift* 45, 97–106.
- HAIRAPETIAN V, BLOM H & MILLER C G 2008. Silurian thelodonts from the Niur Formation, central Iran. *Acta Palaeontologica Polonica* 53, 85–95.
- HAIRAPETIAN V & GINTER M 2009. Pelagic chondrichthyan microremains from the Upper Devonian of the Kale Sardar section, eastern Iran. *Acta Geologica Polonica* 60, 357–371.
- HAIRAPETIAN V, ROELOFS B, TRINAJSTIC K & TURNER S (in press) Famennian survivor turiniid thelodonts of North and East Gondwana. In: Koenigshof P & Becker T (eds) *Devonian climate, sea-level and evolutionary events*. *Geological Society of London Special Publication*.

- HANSMA J, TOHVER E, YAN E, TRINAJSTIC K, ROELOFS B, PEEK S, SLOZNICK S, KIRSCHVINK J, PLAYTON T, HAINES P & HOCKING R (in press) Late Devonian carbonate magnetostratigraphy from the Oscar and Horse Spring Ranges, Lennard Shelf, Canning Basin, Western Australia. *Earth and Planetary Science Letters*.
- HAY O 1909. On the nature of *Edestus* and related genera, with descriptions of one new genus and three new species. *Proceedings United States National Museum* 37, 43–61.
- HEINTZ A 1932. The structure of *Dinichthys*: a contribution to our knowledge of the Arthrodira. In: Gudger E (ed.) *The Bashford Dean Memorial Volume: Archaic Fishes*, pp. 115–224. American Museum of Natural History, New York.
- HOCKING R M 1990. Carnarvon Basin. In: *Geology and Mineral Resources of Western Australia*, pp. 457–495. Geological Survey of Western Australia Memoir 3.
- HOCKING R M, MOORS H T & VAN DE GRAAFF J E 1987. Geology of the Carnarvon Basin, Western Australia. *Geological Survey of Western Australia Bulletin* 133.
- HOCKING R M, PLAYFORD P E, HAINES P.W. & MORY A J 2008. Paleozoic geology of the Canning Basin—a field guide *Geological Survey of Western Australia Record* 2008/18.
- HOLLAND T 2013. Pectoral girdle and fin anatomy of *Gogonassus andrewsae* Long 1985: implications for tetrapodomorph limb evolution. *Journal of Morphology* 274, 147–164.
- HOLLAND T & LONG J A 2009. On the phylogenetic position of *Gogonassus andrewsae* Long J. 1985, within the Tetrapodomorpha. *Acta Zoologica* 90, 285–96
- JARVIK E 1980. *Basic structure and evolution of vertebrates*. Academic Press, London.
- JOHANSON Z 2003. Placoderm branchial and hypobranchial muscles and origins in jawed vertebrates. *Journal of Vertebrate Paleontology* 23, 735–749.
- JOHANSON Z & TRINAJSTIC K 2014. Fossilized ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes. *Palaeontology* DOI: 10.1111/pala.12093.
- JONES P, METCALFE I, ENGEL B A, PLAYFORD G, RIGBY J, ROBERTS J, TURNER S & WEBB G E 2000. Carboniferous palaeobiogeography of Australasia. In: Wright A J, Young G C, Talent J A & Laurie J R (eds) *Palaeobiogeography of Australasian faunas and floras*, pp. 259–286. Memoir of the Association of Australasian Palaeontologists 23.
- KARPINSKY A P 1899. On the edestid remains and its new genus *Helicoprion*. *Zapiski Imperatorski Akademii Nauk* 7, 1–67 (in Russian).
- KARPINSKY A P 1912. On *Helicoprion* and other Edestidae. *Proceedings of the Russian Mineralogical Society* 49, 69–94 (in Russian).
- KLAPPER G 1989. The Montagne Noire Frasnian (Upper Devonian) conodont succession. In: McMillan N J, Embry A F & Glass D J (eds) *Devonian of the World*, vol 3, pp. 449–468. Canadian Society of Petroleum Geologists Memoir 14.
- LONG J A 1985. A new osteolepidid fish from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* 12, 361–377.
- LONG J A 1986. A new Late Devonian acanthodian fish from Mt. Howitt, Victoria, Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society of Victoria* 98, 1–17.
- LONG J A 1987. A new dinichthyid fish (Placodermi: Arthrodira) from the Upper Devonian of Western Australia, with a discussion of dinichthyid interrelationships. *Records of the Western Australian Museum* 13, 515–540.
- LONG J A 1988. Late Devonian fishes from Gogo, Western Australia *National Geographic Research* 4, 436–449.
- LONG J A 1990. Late Devonian chondrichthyans and other microvertebrate remains from northern Thailand. *Journal of Vertebrate Paleontology* 10, 59–71.
- LONG J A 1991. The long history of Australian fossil fishes. In: Vickers-Rich P, Monaghan J M, Baird R F & Rich T H (eds) *Vertebrate palaeontology of Australasia*, pp. 337–428. Pioneer Design Studio, Melbourne.
- LONG J A 1993. Palaeozoic vertebrate biostratigraphy of South-East Asia and Japan. In: Long J A (ed.) *Palaeozoic vertebrate biostratigraphy and biogeography*, pp. 277–289. Belhaven Press, London.
- LONG J A 1995. *The rise of fishes*. The Johns Hopkins University Press, Baltimore.
- LONG J A 2004. *Gogo fish! The story of the Western Australian State Fossil emblem*. Western Australian Museum, Perth.
- LONG J A 2006. *Swimming in Stone: The Amazing Gogo Fossils of the Kimberley*. Fremantle Press, Perth.
- LONG J A & TRINAJSTIC K 2000. Devonian microvertebrate faunas of Western Australia. In: Blicek A & Turner S (eds) *Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*, pp. 471–486. Courier Forschungsinstitut Senckenberg 223.
- LONG J A & TRINAJSTIC K 2010. The Late Devonian Gogo Formation Lagerstätte of Western Australia: exceptional early vertebrate preservation and diversity. *Annual Review of Earth and Planetary Sciences* 38, 255–279.
- LONG J A, TRINAJSTIC K & JOHANSON Z 2009. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature* 457, 1124–1127.
- LONG J A, TRINAJSTIC K, YOUNG G C & SENOEN T 2008. Live birth in the Devonian period. *Nature* 453, 650–652.
- LONG J A, YOUNG G C, HOLLAND T, SENDEN T & FITZGERALD E M G 2006. An exceptional Devonian fish sheds light on tetrapod evolution. *Nature* 444, 199–202.
- MACAOIE C I 2002. Thelodont fish and conodonts from the Lower Devonian of Reefton, New Zealand. *Alcheringa* 26, 423–433.
- MAWSON R, TALENT J A, BEAR V C, BENSON D S, BROCK G A, FARRELL J R, HYLAND K A, PYEMONT B D, SLOAN T R, SORENTINO L, STEWART M I, TROTTER J A, WILSON G A & SIMPSON A G 1988. Conodont data in relation to resolution of Stage and zonal boundaries for the Devonian of Australia. In: McMillan N J, Embry A F & Glass D J (eds) *Devonian of the World*, vol 3, pp. 485–527. Canadian Society of Petroleum Geologists Memoir 14.
- MCMAMARA K, FEIST R & EBACH M 2009. Patterns of evolution and extinction in the last harpetid trilobites during the Late Devonian (Frasnian). *Palaeontology* 52, 11–33.
- MELLENDEZ I, GRICE K, TRINAJSTIC K, LADJAVARDI M, GREENWOOD P & THOMPSON K 2013. Biomarkers reveal the role of photic zone euxinia in exceptional fossil preservation: an organic geochemical perspective. *Geology* 41, 123–126.
- MILES R S 1967. Observations on the ptyctodont fish *Rhamphodopsis* Watson. *Zoological Journal of the Linnean Society of London* 47, 99–120.
- MILES R S 1969. Features of placoderm diversification and the evolution of the arthrodire feeding mechanism. *Transactions of the Royal Society of Edinburgh* 68, 123–170.
- MILES R S 1971. The Holonematidae (placoderm fishes): a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society B* 263, 101–234.
- MILES R S & YOUNG G C 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo Western Australia. *Linnean Society of London Symposium Series* 4, 123–198.
- MOORS H T 1981. An alluvial fan-fluvial plain depositional model for the Devonian Willaraddie Formation and Manubia sandstone of the Carnarvon Basin, W.A. *Geological Survey of Western Australia Annual Report for 1980*, 62–67.
- NICOLL R S 1977. Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics* 2, 217–278.

- NICOLL R. 1979. A Late Devonian age for the Munabia Sandstone, Carnarvon Basin, W.A. *Bureau of Mineral Resource, Professional Oil Geology* 79/034 (unpubl.).
- ØRVIG T 1960. New finds of acanthodians, arthrodires, crossopterygians, ganoids and dipnoans in the upper Middle Devonian Calcareous Flags (Oberer Plattenkalk) of the bergisch-Paffrath Trough. (Part 1). *Paläontologische Zeitschrift* 34, 295–335.
- PATTERSON C 1965. The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society B* 249, 101–219.
- PARKES R 1995. Late Silurian–Early Devonian vertebrate microremains from Nevada and southeastern Australia: biochronology, biogeography and application of novel histological techniques. BSc (Hons) thesis, Macquarie University, North Ryde (unpubl.).
- PLAYFORD P E, HOCKING R M & COCKBAIN A E 2009. Devonian reef complexes of the Canning Basin, Western Australia. *Geological Survey of Western Australia Bulletin* 145.
- QU Q, SANCHEZ S, BLUM H, TAFFOREAU P & AHLBERG P 2013a. Scales and tooth whorls of ancient fishes challenge distinction between external and oral ‘teeth’ *PLoS One* 8 (8), e71890.
- QU Q, ZHU M & WANG W 2013b. Scales and dermal skeletal histology of an early bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales and hard tissues. *PLoS ONE* 8, e61485.
- RITCHIE A 1973. *Wuttagoonaspis* gen. nov., an unusual arthrodire from the Devonian of western New South Wales, Australia. *Palaeontographica A* 143, 58–72.
- RITCHIE A 1975. *Groenlandaspis* in Antarctica, Australia and Europe. *Nature* 254, 569–574.
- RITCHIE A & GILBERT-TOMLINSON J 1977. First Ordovician vertebrates from the Southern Hemisphere *Atcheringa* 1, 351–368.
- ROELOFS B, TRINAJSTIC K, PLAYTON T E, TOHVER E, HAINES P, HOCKING R, BARHAM M, HANSMIA J, HILLBUN K, GRICE K, MAODU Y, RATCLIFFE K, PISAREVSKY S & MONTGOMERY P 2013. Vertebrate biostratigraphy from the Devonian and Carboniferous in the Canning Basin, Western Australia. In: Keep M & Moss S J (eds) *The Sedimentary Basins of Western Australia* 4, Abstracts. Proceedings of the Petroleum Exploration Society of Australia Symposium, Perth, WA, 2013.
- RÜCKLIN M, DONOGHUE P C J, JOHANSON Z, TRINAJSTIC K, MARONE F & STAMPANONI M 2012. Development of teeth and jaws in the earliest jawed vertebrates. *Nature* 491, 748–751.
- SANCHEZ S, AHLBERG P E, TRINAJSTIC K M, MIRONE A & TAFFOREAU P 2012. Three-dimensional synchrotron virtual paleohistology: a new insight into the world of fossil bone microstructures. *Microscopy and Microanalysis* 18, 1095–1105.
- SANCHEZ S, DUPRET V, TAFFOREAU P, TRINAJSTIC K M, RYLL B, GOUTTENNOIRE P-J, WRETMIAN L, ZYLBERBERG L, PEYRIN F & AHLBERG P E 2013. 3D Microstructural architecture of muscle attachments in extant and fossil vertebrates revealed by Synchrotron Microtomography. *PLoS ONE* 8, e56992.
- SANSOM I J, HAINES P W, ANDREEV P & NICOLL R S 2013. A new pteraspidomorph from the Nihil Formation (Katian, Late Ordovician) of the Canning Basin, Western Australia. *Journal of Vertebrate Paleontology* 33, 764–769.
- SANSOM I J, MILLER G C, HEWARD A, DAVIES N S, BOOTH G A, FORTEY R A & PARIS F 2009. Ordovician fish from the Arabian peninsular. *Palaeontology* 52, 337–342.
- SEDDON G 1969. Conodont and fish remains from the Gneudna Formation, Carnarvon Basin, Western Australia. *Journal of the Royal Society of Western Australia* 52, 21–30.
- SHEN J, WEBB G & JELL J 2008. Platform margins, reef facies, and microbial carbonates; a comparison of Devonian reef complexes in the Canning Basin, Western Australia, and the Guilin region, South China. *Earth-Science Reviews* 88, 33–59.
- SMITH M & JOHANSON Z 2003. Separate evolutionary origins of teeth from evidence in fossil jawed vertebrates. *Science* 299, 1235–1236.
- STRUCKMEYER H I M and TOTTERDELL J M (Editors) 1992. *Australia, Evolution of a Continent / BMR Palaeogeographic Group*. Australian Government Publishing Service, Canberra.
- TAPANILA L, PRUITT J, PRADEL A, WILGA C, RAMSAY J, SCHLADER R, DIDIER D. 2013. Jaws for a spiral tooth whorl: CT images reveal novel adaptation and phylogeny in fossil *Helicoprion*. *Biology Letters* doi 10.1098/rsbl.2013.0057.
- THOMAS G A 1957. Lower Carboniferous deposits in the Fitzroy Basin, Western Australia. *Australian Journal of Science* 19, 160–161.
- TRINAJSTIC K 1999a. New anatomical information on *Holonema* (Placodermi) based on material from the Frasnian Gogo Formation and the Givetian–Frasnian Gneudna Formation, Western Australia. *Geodiversitas* 21, 69–84.
- TRINAJSTIC K 1999b. Scales of palaeoniscoid fishes (Osteichthyes: Actinopterygii) from the Late Devonian of Western Australia *Records of the Western Australian Museum Supplement* 57, 93–106.
- TRINAJSTIC K 1999c. Scale morphology of the Late Devonian palaeoniscoid *Moythomasia durgaringa* Gardiner and Bartram, 1977. *Atcheringa* 23, 9–19.
- TRINAJSTIC K 2000. Conodonts, thelodonts and phoebodonts— together at last *Geological Society Of Australia Abstracts* 61, 121.
- TRINAJSTIC K 2001a. A description of additional variation seen in the scale morphology of the Frasnian thelodont *Australolepis seddoni* Turner and Dring, 1981. *Records of the Western Australian Museum Supplement* 20, 237–246.
- TRINAJSTIC K 2001b. Acanthodian microremains from the Frasnian Gneudna Formation, Western Australia. *Records of the Western Australian Museum Supplement* 20, 187–198.
- TRINAJSTIC K, BOISVERT C, LONG J, MAKSIMENKO A, JOHANSON Z in press a. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biological Reviews*
- TRINAJSTIC K & GEORGE A D 2009. Microvertebrate biostratigraphy of Upper Devonian (Frasnian) carbonate rocks in the Canning and Carnarvon basins of Western Australia. *Palaeontology* 52, 641.
- TRINAJSTIC K, GRICE K, DOWNES P, BÖTTCHER M, MELENDEZ J, DELLWIG O, BURROW C & VERRALL M in press b. Mineralized muscles and organs in a 380 million year old actinopterygian fish from the Gogo Formation, Western Australia. *PLoS ONE*.
- TRINAJSTIC K & JOHANSON J 2014. Fossilized ontogenies: the contribution of placoderm ontogeny to our understanding of the evolution of early gnathostomes *Palaeontology* 57, 505–516.
- TRINAJSTIC K & LONG J A 2009. A new genus and species of ptyctodont (Placodermi) from the Late Devonian Gneudna Formation, Western Australia, and an analysis of ptyctodont phylogeny. *Geological Magazine* 146, 743–760.
- TRINAJSTIC K, LONG J, JOHANSON Z, YOUNG G & SENDEN T 2012. New morphological information on the ptyctodontid fishes (Placodermi, Ptyctodontida) from Western Australia. *Journal of Vertebrate Paleontology* 32, 757–780.
- TRINAJSTIC K, MARSHALL C, LONG J A, BIFIELD K 2007. Exceptional preservation of nerve and muscle tissues in Late Devonian placoderm fish and their evolutionary implications. *Biology Letters* 3, 197–200.
- TRINAJSTIC K, SANCHEZ S, DUPRET V, TAFFOREAU P, LONG J, YOUNG G, SENDEN T, BOISVERT C, POWER N & AHLBERG P E 2013. Fossil musculature of the most primitive jawed vertebrates. *Science* 341, 160–164.
- TURNER S 1982a. Thelodonts and correlation. In: Rich P V & Thompson E M (eds) *The Fossil Vertebrate Record of Australasia*, pp. 128–132. Monash University Offset Printing Unit, Clayton.
- TURNER S 1982b. Middle Palaeozoic elasmobranch remains from Australia. *Journal of Vertebrate Paleontology* 2, 117–131.
- TURNER S 1990. Early Carboniferous shark remains from the Rockhampton District, Queensland. *Memoirs of the Queenstaud Museum* 28, 65–73.

- TURNER S 1991. Palaeozoic vertebrate microfossils in Australasia. In: Vickers-Rich P, Monaghan J M, Baird R F & Rich T H (eds) *Vertebrate palaeontology of Australasia*, pp. 429–464. Pioneer Design Studio, Melbourne.
- TURNER S 1993. Palaeozoic microvertebrate biostratigraphy of Eastern Gondwana. In: Long J A (ed.) *Palaeozoic vertebrate biostratigraphy and biogeography*, pp. 174–207. Belhaven Press, London.
- TURNER S 1995. Defining Devonian and D/C microvertebrate faunal assemblages or zones for eastern Gondwana. In: Turner S (ed.) *Palaeozoic Microvertebrates 1995 Report: Moscow-94 Workshop*, pp. 43–52. Ichthyolith Issues Special Publication 1.
- TURNER S 1997. Sequence of Devonian thelodont scale assemblages in East Gondwana. In: Klapper G, Murphy M A & Talent J A (eds) *Paleozoic sequence stratigraphy, biostratigraphy, and biogeography: studies in honor of J. Granville ("Jess") Johnson*, pp. 295–315. Geological Society of America Special Publication 321.
- TURNER S 2009. Fossil Lagerstätten in Australia: discovery and politics. In: Pemberton G (ed.) *INHIGEO 34 Fossils & Fuels, Abstracts*, pp. 73–74. University of Calgary, August 10–14 2009.
- TURNER S 2014. *Report on Silurian and Devonian microvertebrates from Western Australian boreholes*. Report to Geological Survey of Western Australia (unpubl.).
- TURNER S, BASDEN A & BURROW C J 2000. Devonian vertebrates of Queensland. In: Blicek A & Turner S (eds) *Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*, pp. 487–522. Courier Forschungsinstitut Senckenberg 223.
- TURNER S, BLIECK A R M & NOWLAN G S 2004. Cambrian–Ordovician vertebrates. In: Webby B D, Droser M, Feist R & Percival I (eds) *IGCP410 The Great Ordovician Biodiversity Event*, pp. 327–335. Columbia University Press, New York.
- TURNER S, BURROW C J, GHOLAMALIAN H & YAZDI M 2002. Late Devonian (early Frasnian) microvertebrates and conodonts from the Chahriseh area near Esfahan, Iran. *Memoirs of the Association of Australasian Palaeontologists* 27, 149–159.
- TURNER S & DRING R S 1981. Late Devonian thelodonts (Agnatha) from the Gneudna Formation, Carnarvon Basin, Western Australia. *Alcheringa* 5, 39–48.
- TURNER S, with contributions from JONES R, LEU M, LONG J A, PALMIERI V & STEWART I 1994. IGCP 328: Carboniferous shark remains of Australia. In: Mawson R & Talent J A (eds) *APC-94 (papers from the First Australian Palaeontological Convention, Macquarie University, 7–9 February 1994, Abstracts*, p. 58.
- TURNER S, TRINAJSTIĆ K, HAIRAPETIAN V, JANVIER P & MACADIE I 2004. Thelodonts from western Gondwana. In: Richter M & Smith M M (eds) *10th International Symposium on early vertebrates/lower vertebrates. Gramada, Brazil, 24–28 May 2004. Programme and Abstracts*, pp. 45–46. UFRGS & Sociedade Brasileira de Paleontologia.
- TURNER S, VERGOOSSEN J M J & YOUNG G C 1995. Fish microfossils from Irian Jaya. *Memoirs of the Australasian Association of Palaeontologists* 18, 165–178.
- UPENIECE I 1996. *Lodeacanthus gaugicus* n. g. et sp. (Acanthodii: Mesacanthidae) from the Late Devonian of Latvia. *Modern Geology* 20, 383–398.
- VERGOOSSEN J M J 1995. Remarks on microremains of acanthodians (Gnathostomata) from the late Pridoli of Manbrook (Upper Silurian, Great Britain). *Geobios* 28, 399–401.
- WANG S & TURNER S 1995. A reappraisal of Upper Devonian–Lower Carboniferous vertebrate microfossils in South China. *Professional Papers of Stratigraphy and Palaeontology* 26, 59–70.
- WATSON D M S 1934. The interpretation of arthrodires. *Proceedings of the Zoological Society of London* 3, 437–464.
- WATSON D M S 1938. On *Rhamphodopsis*, a ptyctodont from the Middle Old Red Sandstone of Scotland. *Transactions of the Royal Society of Edinburgh* 59, 397–410.
- YOUNG G C 1986. The relationships of placoderm fishes. *Zoological Journal of the Linnean Society of London* 88, 1–56.
- YOUNG G C 1987. Devonian fish remains from Billiluna, eastern Canning Basin, Western Australia. *BMR Journal of Australian Geology & Geophysics* 10, 179–192.
- YOUNG G C 1991. The first armoured agnathan vertebrates from the Devonian of Australia. In: Chang M-M, Liu Y-H & Zhang G-R (eds) *Early vertebrates and related problems of evolutionary biology*, pp. 67–85. Science Press, Beijing.
- YOUNG G C 1993. Middle Palaeozoic macrovertebrate biostratigraphy of Eastern Gondwana. In: Long J A (ed.) *Palaeozoic vertebrate biostratigraphy and biogeography*, pp. 208–251. Belhaven Press, London.
- YOUNG G C 1997. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. *Journal of Vertebrate Paleontology* 17, 1–25.
- YOUNG G C 2005. An articulated phyllolepid fish (Placodermi) from the Devonian of central Australia: implications for non-marine connections with the Old Red Sandstone continent. *Geological Magazine* 142, 173–186.
- YOUNG G C 2009. New arthrodires (Family Williamsaspididae) from Wee Jasper, New South Wales (Early Devonian), with comments on placoderm morphology and palaeoecology. *Acta Zoologica* 90, 69–82.
- YOUNG G C, BURROW C J, LONG J A, TURNER S & CHOO B 2010. Devonian macrovertebrate assemblages and biogeography of East Gondwana (Australasia, Antarctica). *Palaeoworld* 19, 55–74.
- YOUNG G C & GOUJET D 2003. Devonian fish remains from the Dulcie Sandstone and Cravens Peak Beds, Georgina Basin, central Australia. *Records of the Western Australian Museum Supplement* 65, 1–85.
- YOUNG G C, KARATAJUTE-TALIMAA V & SMITH M M 1996. A possible Late Cambrian vertebrate from Australia. *Nature* 383, 810–812.
- YOUNG G C & TURNER S 2000. Devonian microvertebrates and marine nonmarine correlation in East Gondwana: overview. In: Blicek A & Turner S (eds) *Palaeozoic vertebrate biochronology and global marine/non-marine correlation. Final report of IGCP 328 (1991–1996)*, pp. 453–470. Courier Forschungsinstitut Senckenberg 223.
- YOUNG G C, TURNER S, OWEN M, NICOLL R S, LAURIE J R & GORTER J D 1987. A new Devonian fish fauna, and revision of post-Ordovician stratigraphy in the Ross River Syncline, Amadeus Basin, central Australia. *BMR Journal of Australian Geology & Geophysics* 10, 233–242.
- ZHU M, YU X B, AHLBERG P E, CHOO B, LU J, QIAO T, ZHAO W, JIA L, BLUM H & ZHU Y A 2013. Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* 502, 188–193.

Received 22 February 2014; accepted 1 June 2014